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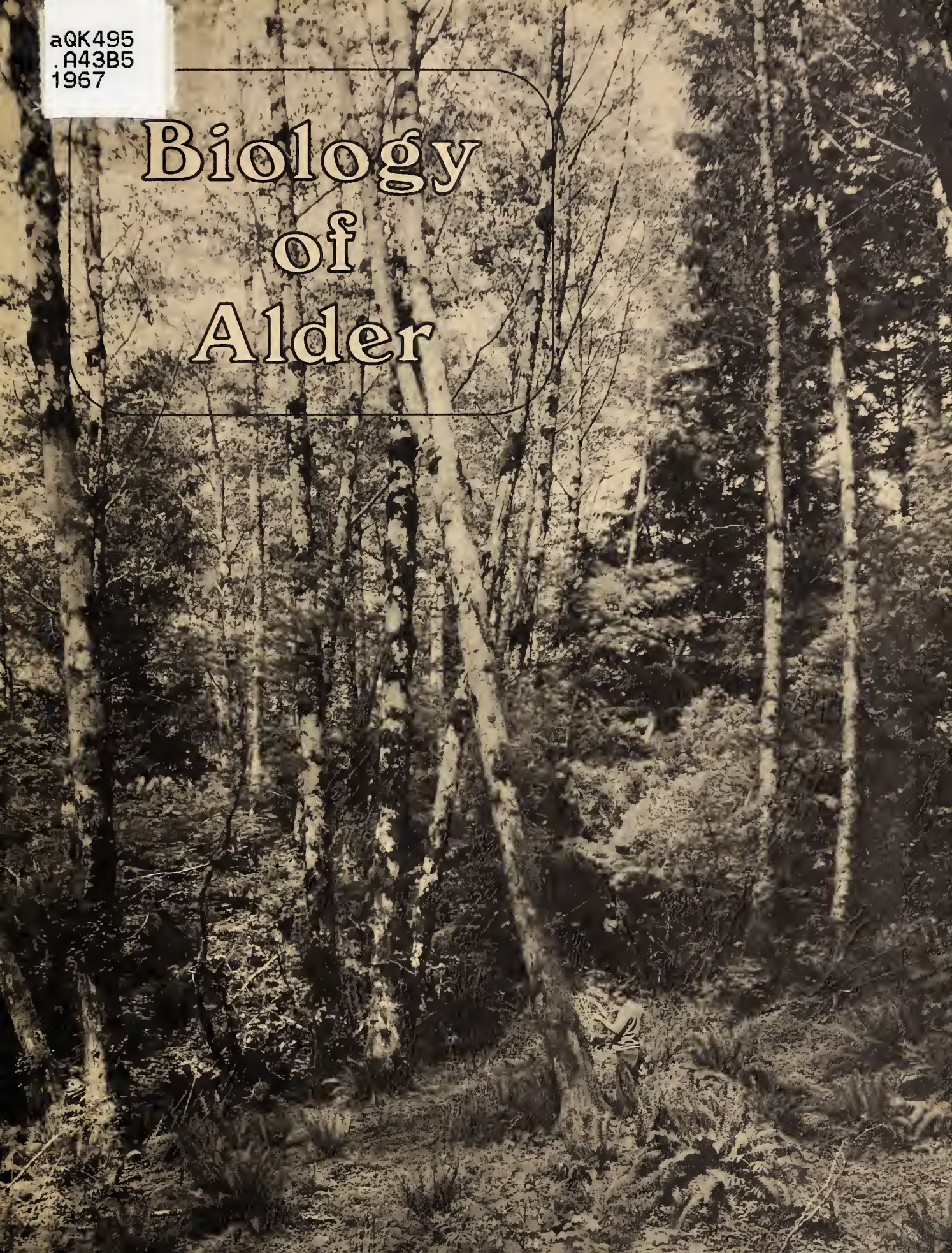
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Biology
of
Alder

Cover photo:
 A stand of red alder at Cascade Head Experimental Forest near
  Otis, Oregon. The trees are from 14 to 20 inches in diameter.
(U.S. Forest Service photo 325534)

Biology of Alder

Proceedings of a Symposium
held at
NORTHWEST SCIENTIFIC ASSOCIATION Fortieth Annual Meeting
Pullman, Washington
April 14-15, 1967

Edited by
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R. F. Tarrant
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Editors' Foreword

In the Western United States, man's regard for alders in times past was characterized by cheerful appreciation. Dr. A. Kellogg extolled *Alnus rubra* Bong. in this way in the nineteenth century:[1]

> *they also maintain their broad leaves so perfectly horizontal, and the spreading branches so nearly so, as to afford one among the finest, most open, and airiest of canopies—what was designated of old as the dense 'fat shadows,' beneath which the green grass and the tender herb continued to flourish...Like the willows, their multiplied shallow roots preserve margins from the wear and tear of aggressive streams, and during the hotter portions of the year, shelter, cool, and sweeten them, and together with the falling leaves, infuse and tone sluggish and stagnant waters. It is certainly worthy of special note, that like most mineral waters, stock always relish these discolored pools best. The flesh of trout, then and there, acquires an aldery-tinged color and quality. The leaves are of some repute as fodder, the bark for tanning, and with twigs, tags, and young wood, as a tonic, in teas, beers, etc.; for diseases of the skin, as detersive and expectorant, and a gargle in ailments of the throat; for ointments, etc.; colors green, red, brown, yellow, and black, and sundry intermediate tints, according to the treatment.*

Since Kellogg's day and particularly in the last 20 years, however, forest management has become increasingly intensive. In striving for higher yields of currently more valuable tree species such as Douglas-fir, forest managers have sometimes regarded alders as weeds. Though the soil-improving quality of alder may be acknowledged, suppression of more valuable conifers by alders is more often than not judged economically intolerable.

Recent research on beneficial effects of alders on associated conifers provides the forest manager with additional food for thought. Soon foresters may find it economically and biologically desirable to manage *for* alder on selected sites or in selected situations. This symposium was organized to bring together reports on contemporary research with alder. It provides, to a degree, a status report on the biology of alder and the art of managing it.

All but four of the papers presented at the symposium are included in these proceedings. One of these, "Phytotaxonomical and geobotanical studies on the genus *Alnus*," by Saburo Murai, is already available in published form[2] and constitutes the outstanding taxonomic treatise on *Alnus*.

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[1] Kellogg, A. Forest trees of California. 148 p. 1882. Calif. State Mining Bur., Sacramento.

[2] Murai, Saburo. Phytotaxonomical and geobotanical studies on genus *Alnus* in Japan (III). Taxonomy of whole world species and distribution of each Sect. Bull. [Jap.] Government Forest Exp. Sta. 171, 107 pp., illus. 1964. (With seven-page summary and figure and table captions in English).

To encourage full play of ideas in a symposium, participants should be free of any kind of censorship. This philosophy has been adopted in editing the proceedings. We have suggested improvements, standardized format, and organized the order of presentation. Ultimate responsibility for content and presentation, however, rests solely with the authors of each paper.

We would like to acknowledge the contribution of the Pacific Northwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, in making possible publication of these proceedings. Mrs. Edith Tomkins was of particular assistance in the final phases of preparation.

J. M. Trappe
J. F. Franklin
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of red alder in Idaho

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Abstract

Alnus rubra Bong., red alder, has been collected in several areas in northern Idaho. This is the eastern limit of the species and appears to be a definite disjunct of the Pacific coastal distribution. Development is centered in three main areas and is shown on range maps around Lake Pend Oreille, Bonner Co.; lower Selway-Lochsa Rivers, Idaho Co., and North Fork Clearwater River, Clearwater Co. All of these areas are in the western redcedar-western hemlock vegetational zone; observations on ecological associations are made. Probable hybridization with other alders is reported.

Prior to 1959, red alder (*Alnus rubra* Bong.) was rarely reported from the northern Rocky Mountains. One distribution map (Preston, 1948) extended the range across northern Washington to the Idaho panhandle. Two references, Rehder (1960) and Preston (1947), included northern Idaho in distribution descriptions, but most descriptions and maps omitted northern Idaho. A search of 11 major herbaria revealed four collections by John Leiberg, in 1895-97, to be the only unquestionable red alder sheets from Idaho; these are deposited in U. S. National Herbarium (E. L. Little, personal communication) and are all from sites around Pend Oreille Lake, where Leiberg lived for a period. These collections may be the basis for Rehder's and Preston's conclusions. In 1960, my collections from Lake Pend Oreille, made in 1958 and 1959, were reported to the Forest Service; and this area was subsequently added to red alder distribution maps (Worthington et al., 1962; Fowells, 1965). Since that time, I have discovered other red alder stands and present here a summary of locations and observations of *Alnus rubra* in northern Idaho. Collections from all areas indicated on the maps (Figs. 1, 2, 3) are deposited in the research herbarium of the Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, where further investigations will be made on these disjunct populations of red alder.
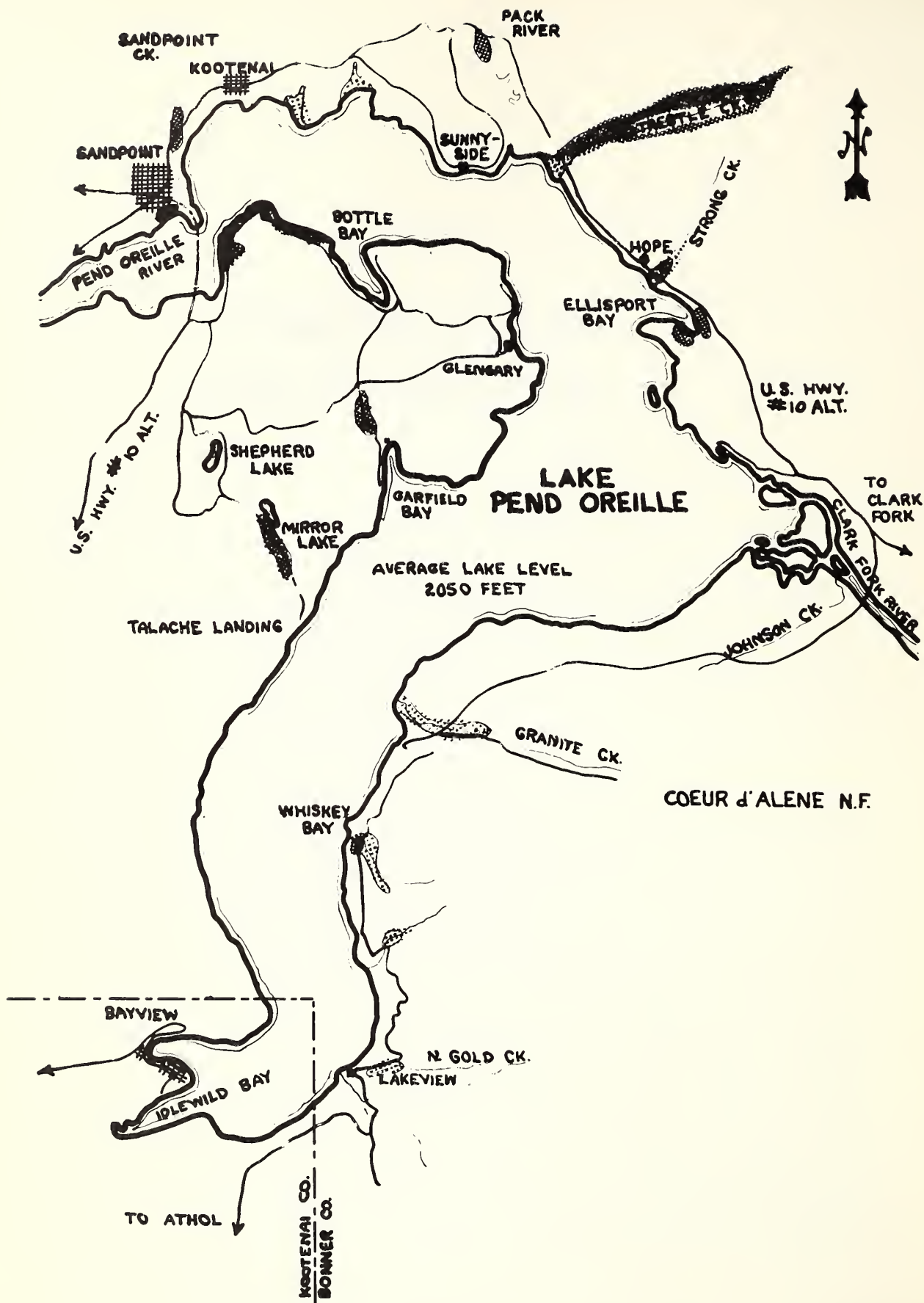
Figure 1. Red alder distribution around Lake Pend Oreille, Idaho.

LAKE PEND OREILLE AREA

Apparently, red alder is mostly restricted to an area within a few miles of the lake, but extending up Trestle Creek at least 5-6 miles. Average lake level is 2,050 ft; most red alders occur within a few hundred ft above this elevation, but are found as high as 3,550 ft on slopes above Trestle Creek. Areas indicated on the distribution map (Fig. 1) are quite accurate; all roads, major stream bottoms, and lake shores in the area have been surveyed. The W and E central shorelines are steep and inaccessible by road, and have not been surveyed, but red alder is expected on perennial streams which flow into the lake.

Distribution. – Centered at lat $47^\circ30'$ N., long $116^\circ45'$ W.; Tps. 53, 54, 55, 56, and 57 N., Rs. 1 and 2 W. and Rs. 1 and 2 E., Boise meridian; Bonner County, Idaho (Fig. 1).

Without exception, the sites indicated were in *Thuja plicata-Tsuga heterophylla/Pachistima myrsinites* associations (Daubenmire, 1952). The usual associated tree species were: *Betula papyrifera* var. *commutata* (Regel.) Fern.,[1] *Thuja plicata* Donn, *Tsuga heterophylla* (Raf.) Sarg., and *Abies grandis* (Dougl.) Lindl.; the first three species are constant associates, except where red alder occurred in pure stands or where the site was disturbed by agricultural or municipal practices. Understory species included *Pachistima myrsinites* (Pursh) Ref. and other members of this union listed by Daubenmire (1952). The most extensive development is along Trestle Creek at the northern end of the lake. Here red alder dominates the streambottom, in many places forming pure stands of trees 15-20 inches in diameter, of good form, and approximately 60-80 ft high. The largest specimen found in the area is 26.8 inches dbh, located near Garfield Bay. In the area immediately surrounding the lake, yet beyond red alder range, there is a noticeable lack of *Alnus tenuifolia* Nutt., thinleaf alder; thus there is little apparent overlap of the two species. A few trees, however, did exhibit some thinleaf alder characteristics, and may be hybrids.

SELWAY, LOCHSA, MIDDLE FORK CLEARWATER RIVERS AREA

Red alder is not as well developed in this area as it is in either the Pend Oreille Lake or N. Fk. Clearwater areas. Suitable habitats are fewer, and this is probably a major factor. Red alder is scattered, chiefly along smaller tributary streams and on lower seepage areas from below Smith Creek on the Middle Fork (about 1,400 ft elev.) to about 10 miles E of Lochsa Ranger Station (Green Flat, elev. 2,400 ft), a total range of some 50 road-miles. It extends up the Selway River at least to road-end near Selway Falls, some 17 miles from the Selway-Lochsa confluence. There are few roads in the area, except on the river bottoms, and an extensive survey of unroaded areas has not been made. The largest tree found was 23.7 inches dbh and about 55 ft tall, located along the Van Camp Road, at 3,600 ft; this, coincidentally, is

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[1] *Scientific names of angiosperms are taken from Hitchcock et al., 1955-64; gymnosperms from Little, 1953; ferns from Flowers, 1950.*
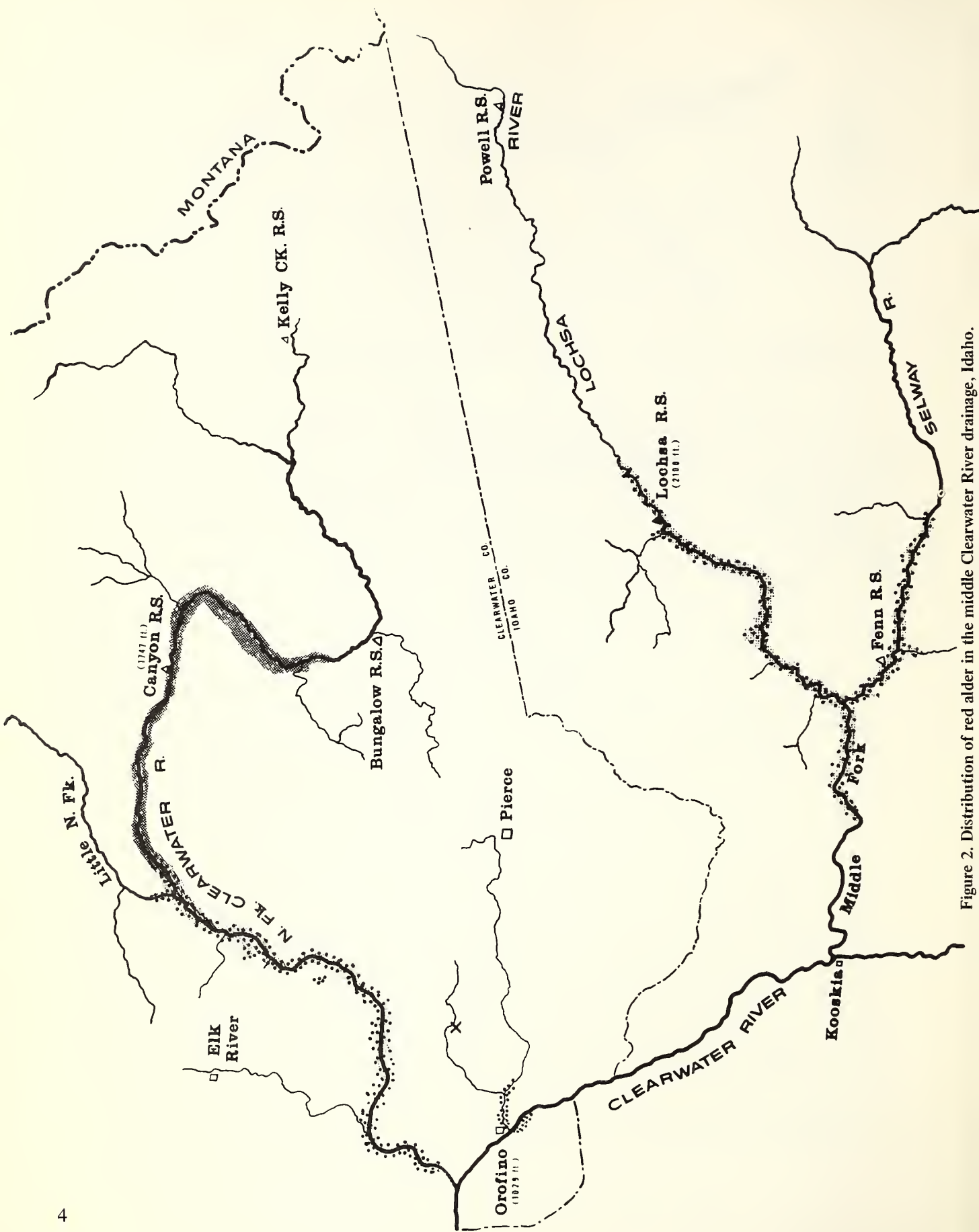
Figure 2. Distribution of red alder in the middle Clearwater River drainage, Idaho.

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the highest elevation at which red alder has been collected in the area. This area has long been known as the only habitat of *Cornus nuttallii* Aud. ex T. & G. (Hitchcock et al., 1961) east of the Cascade Mountains. There are other evidences of Pacific coastal influence, such as tree-like development of *Taxus brevifolia* Nutt. and *Rhamnus purshiana* DC.; both species are usually shrubby in the northern Rocky Mountains but trees in coastal areas. The ranges, here, of *C. nuttallii* and *A. rubra* are almost identical, though their habitats differ. The red alder sites are riparian in a modified *Thuja/Pachistima* habitat; the understory contains no *Pachistima* and is often dominated by *Polystictum munitum* (Kaulf.) Presl. *Cornus stolonifera* var. *occidentalis* (T. & G.) C. L. Hitch.; various *Pachistima* union forbs, and a scattered cover of creeping shrub *Rubus ursinus* Cham. & Schlecht. is almost always present. Associated tree species most frequently include *Thuja plicata, Betula papyrifera* var. *subcordata* (Rydb.) Sarg., *Abies grandis,* and *Rhamnus purshiana.* This area is south of the range of *Tsuga heterophylla* in Idaho. Most of the species listed above are associated with red alder on the coast (Worthington et al., 1962).

The trees in this area vary considerably in their morphology — especially in leaf characteristics. Intergrades with white alder (*Alnus rhombifolia* Nutt.), or thinleaf alder, or both, are apparently present. The nearest stands of un-questioned white alder are but a few miles down the Clearwater River but in an entirely different habitat. Thinleaf alder is present on most of the major tributary streams within the range of red alder, though the two species have not been seen growing together. Murai (1964) reports 23 hybrids in the genus *Alnus.* About half are natural, and of these, 5 are in the Section *Glutinosae,* which contains all three of the alders here discussed; thus, hybridization might be expected. Using leaf inroll, leaf apex, tree form, bark plating, and cone size as strong differentiating features (Johnson, 1968), definite red alder does occur. However, some intergraded forms are undoubtedly present and scattered within the red alder population.

Distribution. — Centered at lat 46° N., long 115°45' W.; Tps. 32, 33, and 34 N., Rs. 5, 6, and 7 E., Boise meridian; Idaho County, Idaho (Fig. 2).

NORTH FORK CLEARWATER RIVER AREA

This area has had a rather superficial examination, but enough to know that extensive red alder development does occur. From a few miles above the confluence of the North Fork with the main Clearwater River to a few miles below Bungalow Ranger Station at some 3,200 ft, a distance of some 80 river miles, there are more or less unbroken stands of red alder along the North Fork and its major tributaries. The area is of immediate interest, since much of the best alder habitat will be inundated in a few years by the reser-voir of Dworshak Dam. One site, on the main Clearwater River near Orofino, appears associated with this area, and is the lowest elevation station for red alder in Idaho at 1,030 ft. Much of the main North Fork river is not accessible by road, and thus has not been examined. During the spring of 1966, the
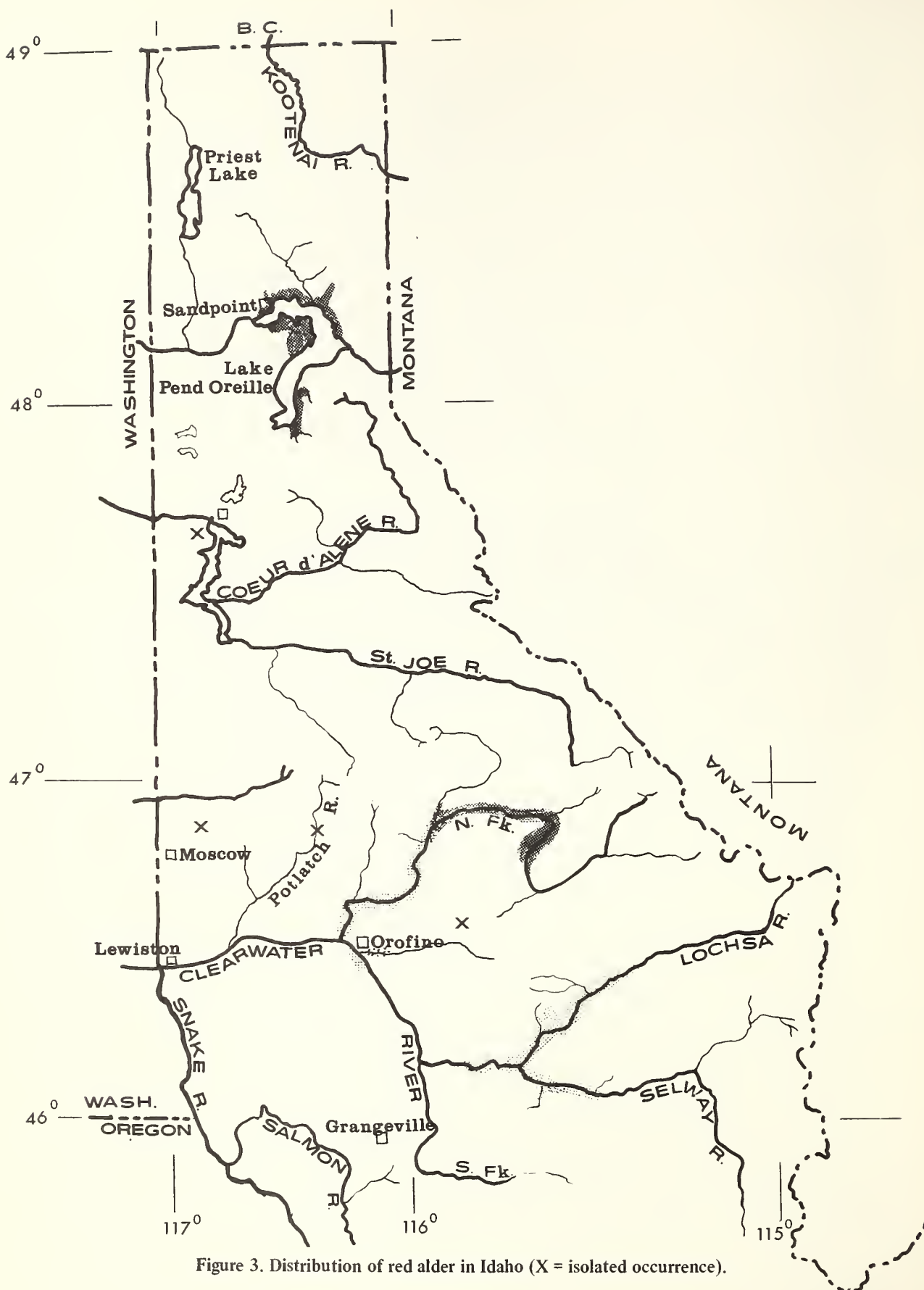
Figure 3. Distribution of red alder in Idaho (X = isolated occurrence).

largest Idaho specimen was located on the North Fork near Skull Creek; it was 35.1 in. dbh and 65 ft high, a respectable size, since until 1966, the world record was 44 in. dbh (Dixon, 1961). This tree was nearly dead, and was removed by road construction in 1966. Best development in the North Fork area occurs in the vicinity of Skull Creek, where red alder is quite abundant on alluvial flats, and also is seen growing several hundred feet above river level (elev. 3,200 ft) as a seral species in the *Thuja/Pachistima* association. Understory vegetation seems generally similar to the Lochsa-Selway area. There is little tree development of *R. purshiana* or *T. brevifolia,* and no *C. nuttallii.*

Ferns are even more conspicuous. *Andiantum pedatum* L., *Polystictum munitum, Pteridium aquilinum* var. *pubescens* Underw. and *Athyrium filix-femina* (L.) Roth are especially abundant and are dominant on many sites. Such areas resemble the *Thuja-Tsuga/Oplopanax* association of Daubenmire (1952) with the *Tsuga* absent and *Oplopanax* dominance taken over by various ferns.

Distribution. — Centered at lat 46°45' N., long 115°50' W.; Tps. 37, 38, 39, 40, and 41 N., Rs. 1, 2, 3, 4, 5, 6, and 7 E., Boise meridian; Clearwater County, Idaho.

MISCELLANEOUS AREAS

Single tree or very small patches of red alder have been collected at several other stations in northern Idaho. Some of these collections appear to be inter-grades, others are undoubtedly red alder (Fig. 3).

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Taxonomy and distribution of northwestern alders

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Abstract

Synonymy, morphological features, and distribution of the four north-western North American species of Alnus — A. rhombifolia, A. rubra, A. tenuifolia, *and* A. sinuata — *are outlined. Included are distribution maps, a synoptic view of vegetative characteristics, and photos of buds and leaves.*

Four species of alder (*Alnus* Ehrhart) are native to northwestern North America. Most sections of this area have at least two species, and many localities have all four species growing in relatively close proximity.

The genus *Alnus* is a member of the subfamily Betulae (Doll.) Aschers. in the family Betulaceae Agardh. Murai (1964) divides *Alnus* into two subgenera and seven sections. The northwestern alders and their intra-generic relationships are shown below:

Subgenus *Alnaster* (Spach.) Endl.
    Section *Alnobetula* (Koch) Murai
        Alnus sinuata (Reg.) Rydb.
Subgenus *Gymnothrysus* (Spach.) Reg.
    Section *Glutinosae* Murai
        Alnus rhombifolia Nutt.
        Alnus rubra Bong.
        Alnus tenuifolia Nutt.

Cone characteristics of the two sections are shown in Figure 1.

Figure 1. Cone characteristics of sections *Alnobetula* (left) and *Glutinosae* (right).

Figure 2. Distribution of white alder (*Alnus rhombifolia*).

The following summary of nomenclature, distribution, and morphological characteristics is by no means exhaustive but is intended to place northwestern alders in a general reference framework as an introduction to this symposium.

Alnus rhombifolia Nuttall — white alder

White alder is a riparian species of lower elevation forest zones, extending along major streams into non-forested bunchgrass, sagebrush-grass, and chaparral types. Mature trees are generally 2 to 3 ft dbh by 50 to 80 ft high (Preston, 1947; Sudworth, 1908); multiple trunks are common. Maximum size is attained in southern California; the largest individual tree is 43 inches dbh and 93 ft tall (Pomeroy and Dixon, 1966).

Distribution. — From Pacific coastal Baja California (lat $31^O30'$ N), north in the coastal valleys of California to just north of San Francisco Bay; interior foothills of the Coast Ranges and mid to lower slopes of the Sierra Nevada (below 7,000 ft); streamsides above the central valley of California and in the dry, interior valleys of southwest Oregon, and the Willamette Valley (Johnston, 1967; Peck, 1967); east on the lower eastern slopes of the northern Sierra Nevada (below 4,500 ft); but not in western Nevada (La Rivers, 1967); northward on the lower eastern slopes of the Cascades in Oregon (100-4,500 ft) and Washington; extending to southern British Columbia (lat about 50° N, elev. about 1,500 ft) along the Okanogan and Kettle Rivers; eastward along the main tributaries of the Columbia River to lower valleys of southeastern and south-central Washington and northeastern Oregon; reaching its eastern limit in Idaho along the Clearwater River (long 116° W; elev. 1,200 ft), southward in Idaho along the Snake River and tributaries to Mann Creek in Washington County (Fig. 2).

Identification. — White alder is very closely related to red alder and the two species are difficult to differentiate where growing together. Fortunately, the habitats and distribution of the two species do not overlap to any great extent. In the summer, white alder can be relatively easily identified by

Figure 3. Typical mature leaves of alder: *left,* red and white; *right,* thinleaf and Sitka.

leaf characteristics (Figs. 3 and 4; Table 1). Winter characteristics of the two species are very similar and identification must be based on several minor points; white alder has greater tendency to bark plating with smaller buds (Fig. 5) and cones than red alder.

Alnus rubra Bongard — red alder, Oregon alder

> *A. oregona* Nuttall
> *A. incana* var. *rubra* (Bongard) Regel
> *A. rubra* var. *pinnatisecta* Starker

Alnus rubra and *A. oregona* are the only scientific names in common usage. Murai (1964) in his world monograph of alders, recognizes *A. rubra*, as does the U. S. Forest Service Checklist (Little, 1953) and more recent floras (Hitchcock et al., 1964).

Red alder is the largest member of the genus and the most important commercially. It is apparently associated with the western redcedar (*Thuja plicata* Donn.) / western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone throughout its range, except south of San Francisco Bay, where it is riparian in chaparral types. While best development is on alluvial flats and in riparian situations, red alder also grows as a seral species on upland situations in conifer climax habitats (Worthington et al., 1962). On good sites, red alder forms one main stem, a long length of clear bole, and a size of 2 to 3 ft dbh by some 65-100 ft high. Maximum stand density, commercial value, and size are attained in coastal Oregon and Washington. The largest tree recorded is 52.5 inches dbh and 92 ft tall (Pomeroy and Dixon, 1966).

Figure 4. Mature leaf margins of alder: *left,* white and red; *right,* Sitka and thinleaf.
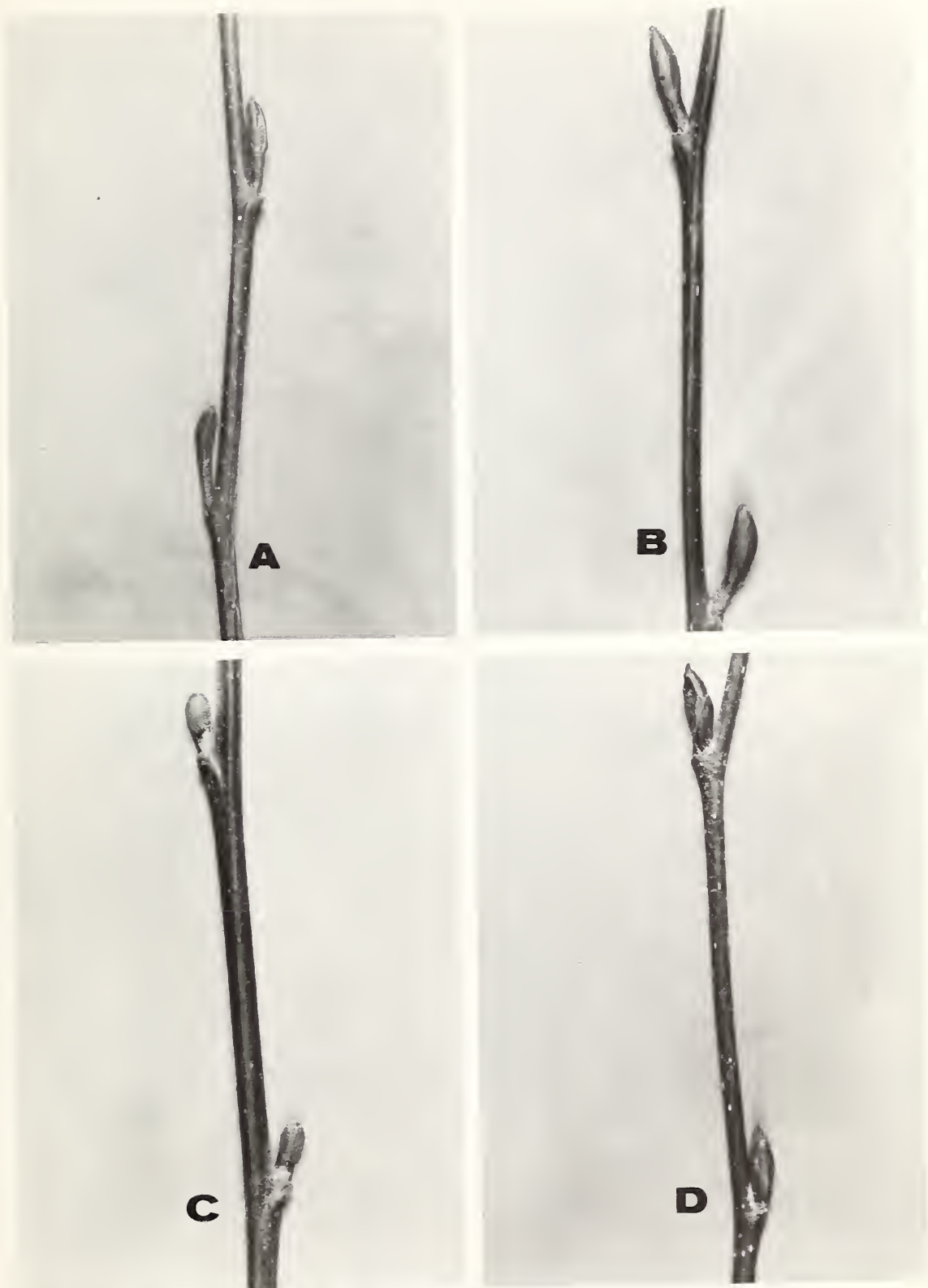
Figure 5. Typical winter buds of alder: *A*, white; *B*, red; *C*, thinleaf; *D*, Sitka.

TABLE 1. Conspectus of northwestern American alders; typical morphological features of high differentiating value for Oregon, Washington, Idaho, Montana, and British Columbia

Scientific name	Winter buds	Leaf apex	Leaf margin	Mature bark	Form	Habitat
Alnus rhombifolia	Stalked; as in A. rubra, but more generally narrow in relation to length; more curved and more closely appressed to the twig	Rounded to broadly acute	Serrate; with teeth tipped by large, dark glands	Plated, reddish-brown in larger trees	Tree – often with several, angled trunks	Lower interior valleys; Douglas-fir, ponderosa pine and treeless zones. Riparian.
Alnus rubra	Stalked; green to reddish; shiny; glabrous; lanceolate to lance-linear; sharp apex	Acute	Obscurely serrate-dentate; definite inroll (revolute); teeth glandular, obscured by inroll	Unplated; grey, (often appearing mottled white due to crustose lichens)	Tree – generally with one, distinct, straight stem	Western red-cedar/western hemlock zone. Riparian and mesic.
Alnus tenuifolia	Stalked; grey to red-brown; dull, short, dense tomentum; ovate to obovate; rounded apex	Acute	Deeply double-dentate (to remotely lobed); small glands on teeth	Unplated, grey	Small tree or large shrub; multiple stems	Upper and/or colder forested zones, uncommonly in high elev. sagebrush. Riparian.
Alnus sinuata	Sessile; lanceolate; sharp apex	Acute	Irregularly serrate	Unplated; grey-green to green	Multiple-stemmed shrub, rarely small tree in coastal areas	Cedar/hemlock or spruce/fir zones. Riparian and mesic.

NOTE: *Bud and leaf size, leaf shape, and pubescence are variable and not considered reliable identifying features.*

Distribution. — From near Santa Barbara along the southern California coast (lat 34° N) northward at lower elevations along the Pacific coast to Yakutat Bay, southeast Alaska (lat 60° N); in this area generally below 2,500 ft and less than 100 miles from the ocean (Worthington et al., 1962). Interior disjuncts have recently been reported from northern Idaho (Johnson, 1966) in low-elevation (1,300-2,200 ft) western redcedar/western hemlock climax habitats around Lake Pend Oreille and along the North Fork of the Clearwater, Lochsa, and Selway Rivers, reaching its eastern limit along the Lochsa at long 115° W (Fig. 6).

Identification. — Red alder is easily confused with white alder, and the differentiation is discussed with white alder and outlined in Table 1. Over-simplified keys may cause confusion between red and thinleaf alder due to overemphasis of leaf characteristics although typical leaves are usually quite distinctive (Fig. 3). Leaf pubescence should not be used; but the inrolled leaf margins of red alder are absent or not well developed on thinleaf and are considered diagnostic for red alder where well developed (Fig. 4). Where margin inroll is poorly developed, winter buds (Fig. 5) are the best vegetative feature to differentiate red from thinleaf alder. Ordinarily, site, elevation, and tree form will provide additional means of separation (Table 1).

An uncommon variant with dissected leaves, from the Portland area of Oregon and southern Washington, has been named variety *pinnatisecta* by Starker (1939).

Alnus tenuifolia Nuttall — thinleaf alder

A. tenuifolia var. *occidentalis* (Dippel) Callier
A. incana ssp. *tenuifolia* Breit.
A. incana ssp. *rugosa* var. *occidentalis* (Dippel) C. L. Hitchcock
A. occidentalis Dippel

The relationship of thinleaf alder to similar alders of eastern North America and Eurasia is a subject of intricate nomenclatural debate. The synonymy above is but a small portion of a long list and is selected to show relationships and to reflect most common usage in northwestern North America. Hultén (1944), Hitchcock et al. (1964), Murai (1964), and Fernald (1945) list synonymy and arguments for various combinations. To clarify the situation for this symposium, I will briefly outline the apparent relationships: The Eurasian species *Alnus incana* (L.) Moench is very similar to eastern North American *A. rugosa* (DuRoi) Spreng. *A. rugosa,* in turn, is often subdivided into several varieties, one of which is var. *serrulata* (Ait.) Winkl. *A. serrulata* (Ait.) Willd. is often recognized as a separate species, and it, too, has several varieties. *A. rugosa* is also similar to *A. tenuifolia* and these species overlap geographically somewhere in west-central Canada. Thus, thinleaf alder is considered by some authors to be a western variety of the eastern *A. rugosa,* whereas others argue that all North American plants are varieties of *A. incana.* Murai (1964) lists the four as separate species: *A. incana, A. rugosa, A. serrulata,* and *A. tenuifolia.*

The map (Fig. 7) outlines the distribution, as determined from a confused synonymy, of the western segment of this complex, here termed *A. tenuifolia.* The *serrulata* group is of swampy sites along the Atlantic coast,
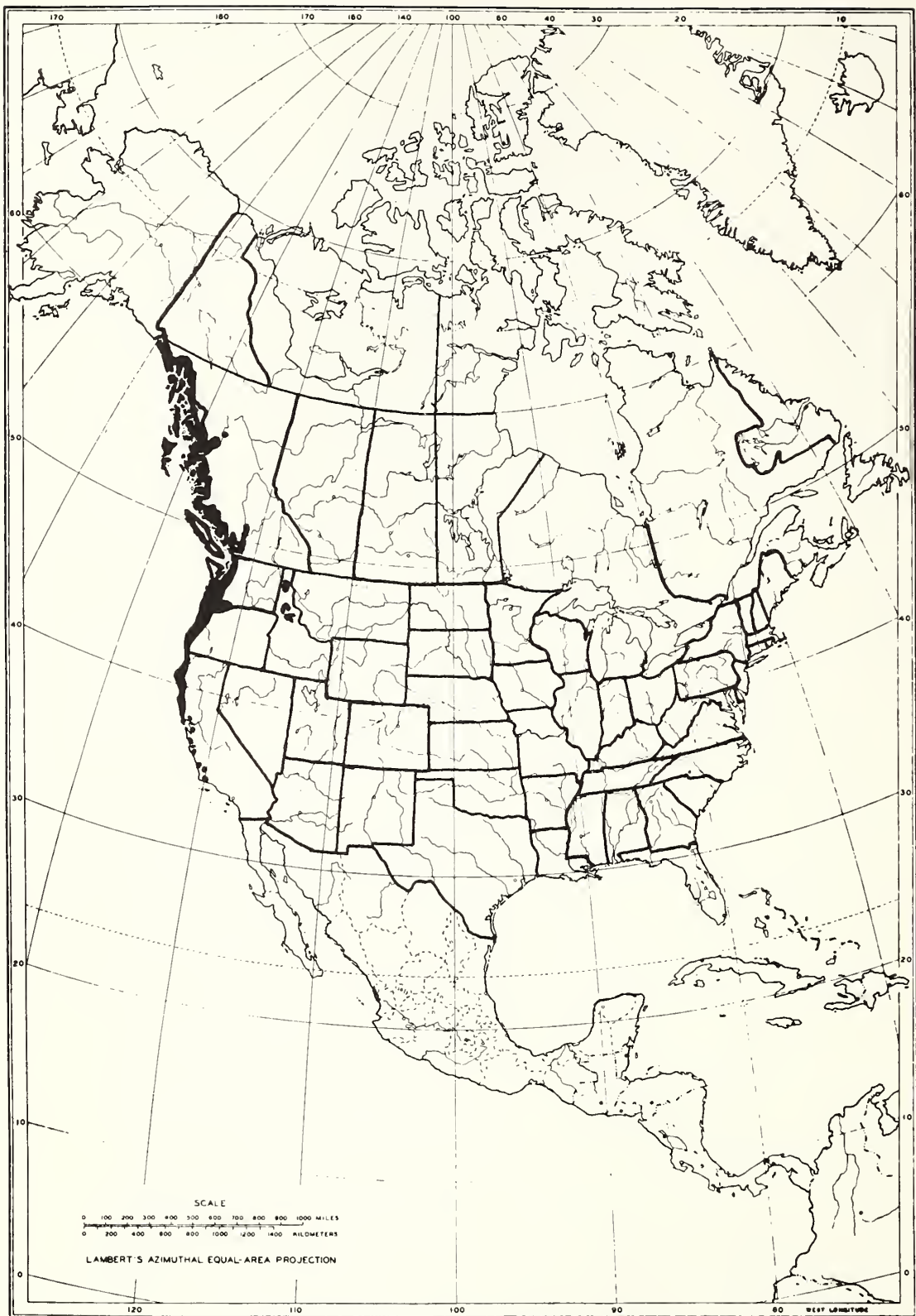
Figure 6. Distribution of red alder (*Alnus rubra*).

southeastern and central conterminous United States and southeastern Canada. The *rugosa* group is of more northern distribution, is chiefly boreal, and associated with spruce/fir and beech/birch/maple climax areas in the northeastern and north-central conterminous United States and eastern and central Canada. The *tenuifolia* group is western in distribution, usually montane, and is discussed in more detail below.

Distribution. — Thinleaf alder is the most widely distributed western North American alder. Generally, it is classed as a large shrub, some 15 to 20 ft high with several stems under 6 inches in diameter. On better sites, it may reach 30 to 40 ft in height and attains diameters near 10 to 12 inches. It is found on a great variety of sites, from near sea level (Alaska) to about 10,000 ft (Arizona, New Mexico, and Colorado). It appears chiefly in forested areas, as a riparian species, or in moist openings within forest zones but does extend into the sagebrush-grass type in the Rocky Mountains (mostly over 5,000 ft). In the Sierra Nevada, it is most common in the subalpine zone (to 8,000 ft), but descends to 4,500 ft through mixed conifer forests (Munz and Keck, 1959). Several authors agree that the southern limit is in Baja California (Preston, 1961; Gleason, 1952; McMinn and Maino, 1946), but Munz and Keck (1959) list Tulare County (lat 37° N) as its southern limit, and this is accepted here. Hitchcock et al. (1964) indicate that it is found in the Cascade Range in both Oregon and Washington, but only on the east slopes. The distribution pattern becomes less certain in British Columbia, but apparently it does not approach the Pacific coast (Taylor, 1967) but is found in southeastern coastal Alaska (Hultén, 1944). The principal development is in the Rocky Mountains, where it reaches its southern limit in the spruce/fir zone (7,000-9,000 ft) of the Rincon Mountains, Arizona (lat 32°20' N) (Mason, 1967); Tidestrom and Kittell (1941) indicate it as present also in the ponderosa and pinyon pine zones of northern Arizona. Martin (1967) indicates its presence in northwestern New Mexico and in the high mountains of the west-central portion of that state. In Nevada, it is restricted to disjuncts in high mountains in the northeast and central portions of the state (La Rivers, 1967). Northward, it is found on suitable habitats, in an almost continuous band in the Rocky Mountains throughout Colorado (5,000-10,000 ft), Utah (7,000-9,000 ft), Montana and Idaho (2,500-8,000 ft), eastern Oregon, eastern Washington, and northward through Alberta, east to Saskatchewan (Porsild, 1967) and northward to Alaska, reaching its northern limit near lat 60° N in the central Yukon River valley (Hultén, 1944) (Fig. 3).

Identification. — Thinleaf alder seldom overlaps in habitat with red alder, and it is doubtful whether it ever is found on the same site with white alder. Winter buds afford the quickest and most reliable difference between thinleaf and both red and white alder (Fig. 5; Table 1).

Alnus sinuata (Regel) Rydberg — Sitka alder, green alder

    Alnus crispa ssp. *sinuata* (Regel) Hultén
    Alnus viridis var. *sinuata* Regel
    Alnus alnobetula (Ehrhart) K. Koch
    Alnus sitchensis Sargent

Figure 7. Distribution of thinleaf alder (*Alnus tenuifolia*).

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Figure 8. Distribution of *Alnus crispa* ssp. *sinuata* and ssp. *crispa* in North America.

The synonymy of Sitka alder is, perhaps, as complicated as that of thin-leaf alder but can be presented here in more condensed form. *Alnus crispa* (Ait.) Pursh is a circumpolar species with several morphological and geographical variants. The subspecies *crispa* Pursh is chiefly Arctic in distribution and is found in central Alaska, across northern Canada, and southward through the Lake States and northeastern conterminous United States as well as in Eurasia. In the southeastern portion of its North American distribution, other varieties may prove to be valid. The subspecies *sinuata* is distributed in coastal western North America from Alaska southward, chiefly with western redcedar/western hemlock and subalpine forests to northern California and southern Idaho. Two other subspecies are confined to Asia. *Alnus viridis* (Chaix) DC., of Europe, is considered by some authors to be synonymous. *A. mollis* Fern. and *A. alnobetula* (in part) of eastern North America = ssp. *crispa* (Murai, 1964).

Distribution. — From northern coastal California (Humboldt Co.; lat 40° N) (Munz and Keck, 1959), northward along coastal Oregon and Washington and in the Cascade Range in those states; apparently rare or absent from the Puget Trough, except at the northern end; across northern Washington to Idaho and central Montana (Booth, 1967); south in Idaho to subalpine areas just north of the Snake River Plains (lat 43° N, 6,000 ft) (several authors list Colorado as the southern limit in the Rocky Mountains, but neither Rydberg (1906) nor Harrington (1954) list it for that state—Porter (1967) says that it is not present in Wyoming.); northward in western Canada, mountain slopes in southwest Alberta (Moss, 1959); north to the Arctic Circle (Porsild, 1967); throughout British Columbia and northward to Alaska near Nome (Hultén, 1944); probably overlapping with ssp. *crispa* from northern Alberta, central MacKenzie, and through most of Alaska, except the southeastern coastal forest (Fig. 8). The map (Fig. 8) is for the two North American subspecies of *A. crispa*. Segregation of the *sinuata* complex north of lat 49° N, was not attempted due to lack of data and confusion in synonymy. However, only *A. sinuata* distribution is reflected in conterminous western U.S.

Identification. — Sitka alder is a shrubby species, rarely becoming a small tree in coastal areas. It is the most cold resistant of the northwestern alders and is often found in subalpine situations, where it is a vigorous invader of talus slopes and seepage areas. In the northern Rocky Mountains, it is found as a seral shrub in the upper and more mesic portions of the western redcedar/western hemlock zone. In areas west of the Cascade summit, Sitka alder appears as both a riparian and a seral forest species, as well as a bog inhabitant near the Pacific coast.

Morphologically, Sitka alder is the most easily recognized of the northwestern North American alders; it is the only species with sessile buds (Fig. 5; Table 1). Inexperienced persons must take care, however, to examine current growth or vigorous shoots, since slow-growing side branches are often one-eighth inch, or less, in length and often give a single bud the appearance of being stalked. Sitka alder leaves are most easily confused with birch, due to shape and leaf serrations (Figs. 3 and 4).

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Relationships of allied species between northwestern U.S.A. and Japan on the genus *Alnus*

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Abstract

In this paper the author has attempted to compare the genus Alnus *in the northwestern United States with that in Japan. The results are reported herein; comments are solicited.*

SPECIES APPEARING IN NORTHWESTERN UNITED STATES AND JAPAN WHICH ARE IN THE SAME SECTIONS

The distribution of alders within East Asia, Japan, and the northwestern and other parts of the United States are classified by subgenera and section in Table 1, according to the new classification system devised by the author (Murai 1962, 1963, 1964). There are 11 known species and four hybrids of alder native to Japan. However, species common to the northwestern United States and Japan are found only in subgenus *Alnaster,* section *Alnobetula,* and subgenus *Gymnothyrsus,* section *Glutinosae.* Therefore these two sections will be considered in detail.

The author investigated species of alder appearing in the northwestern United States through the literature and compared them with alder species occurring in Japan. The results of this comparison together with an outline of distribution are shown in Table 2. Four species occur in the northwestern United States and four species also appear in Japan. Of these, *Alnus crispa,* subspecies *sinuata* in northwestern United States, and *A. crispa,* subspecies *maximowiczii* in Japan, belong to section *Alnobetula.* Three species, *A. tenuifolia, A. rubra* and *A. rhombifolia,* which occur in the northwestern United States, and also three species, *A. matsumurae, A. inokumae* and *A. hirsuta,* which occur in Japan, all belong to section *Glutinosae.*

CLASSIFICATION BY TYPE OF CARPOSQUAMA AND SAMARA

The various external shapes or types of carposquama at the time of ripening, according to the author's previous classification (Murai, 1964), are shown

TABLE 1. Comparative distribution of alders within East Asia, Japan, and United States

Subgenera and section	Distribution			
Subgen. *Alnaster*	Eastern Asia	Japan	Northwestern United States	Other United States
Sect. *Bifurcatus*	–	Japan	–	–
Sect. *Alnobetula*	Siberia	Japan	Northwestern United States	Northern United States
Subgen. *Gymnothyrsus*				
Sect. *Cremastogyne*	Western China	--	–	–
Sect. *Clethropsis*	Western China	--	–	Eastern United States
Sect. *Japonicae*	Southeastern China	Japan	–	Central South America
Sect. *Fauriae*	–	Japan	–	–
Sect. *Glutinosae*	Asia	Eastern Japan	Northwestern United States	Northern United States

TABLE 2. Alder species which occur in the northwestern United States and Japan and which belong in the same sections

Northwestern United States:

Sect. *Alnobetula* — *A. crispa* subspecies *sinuata* — Alaska, British Columbia, northwestern United States.

Sect. *Glutinosae* — *A. tenuifolia* — Alaska, British Columbia northwestern United States.

A. rubra — Alaska, British Columbia, northwestern United States.

A. rhombilfolia — western United States.

Japan:

Sect. *Alnobetula* — *A. crispa* subspecies *maximowiczii* — Okhotsk Sea, Japan, Korea.

Sect. *Glutinosae* — *A. matsumurae* — central Japan.

A. inokumae — north central Japan.

A. hirsuta — Kamchatka, Japan, Baikal, Yakutsk.

in Figure 1. It is apparent that the carposquamas of 29 alder species in the world are classified roughly into 6 types. Only two of these are found in sections common to our district — section *Alnobetula* belongs to type F and all of section *Glutinosae* belongs to type A. Similarly, Figure 2 shows the types of samara which in the alders of the world can roughly be classified into only four types. Of those having a common relation to our districts, section *Alnobetula* belongs to type d, and type a and type b belong to section *Glutinosae*. In addition, *A. maritima,* which is in the eastern United States (section *Clethropsis*), belongs to type c.

Type A (Fig. 1) corresponds to a carposquama having a large height and a triangular central bract; however, in the previous report (Murai, 1964) the shape of bractlet was not taken into consideration. When the shapes of bractlets are investigated for those species appearing in our districts, they can be classified into three subtypes. This bractlet subtype classification is shown in Figure 3. The individual subtypes have the following characteristics:

Subtype AI   bractlet has undulate margins
Subtype AII bractlet has triangular margins
Subtype AIII bractlet has rotund margins

Then the 11 species belonging to section *Glutinosae* are classified by these three subtypes and types of samara, the results are as follows. Those having no relation to our districts are enclosed with brackets. Type of carposquama and samara of *A. oblongifolia* could not be determined because the author had neither specimens nor access to pertinent literature.

AI-a   *A. matsumurae* — one species
AII-b   *A. inokumae, A. tenuifolia*
        (A. rugosa) — three species
AIII-b *A. hirsuta, A. rubra, A. rhombifolia*
        (A. serrulata), (A. glutinosa), (A. incana),
        (A. oblongifolia) — seven species

Distribution of groups of species as classified by carposquama and samara is shown in Table 3. A species belongs to each of the four types in Japan; in the northwestern United States, however, no species belongs to type AI-a, but two species belong to type AIII-b. Species in other districts of North America and in Europe are included for reference totaling two species of section *Alnobetula* and 11 species of section *Glutinosae*.

COMPARISON OF DISTRIBUTION OF SPECIES CLASSIFIED BY TYPE OF CARPOSQUAMA AND SAMARA

The relative distribution of species when classified by type of carposquama and of samara is summarized as follows. The distribution of type F-d (belonging to section *Alnobetula*) is shown in Figure 4. *A. crispa,* a taxon of low height and shrubby habit, is extremely widely distributed around the Northern Hemisphere. Subspecies *sinuata* extends along the western slope of the Rocky Mountains by way of the south coast of Alaska and reaches the Aleutians on the east side of the Pacific. Subspecies *maximowiczii* extends

Figure 1. Author's classification of types of carposquama.

Figure 2. Author's classification of types of samara (seed).

Figure 3. Bractlet supplement to classification of types of carposquama.
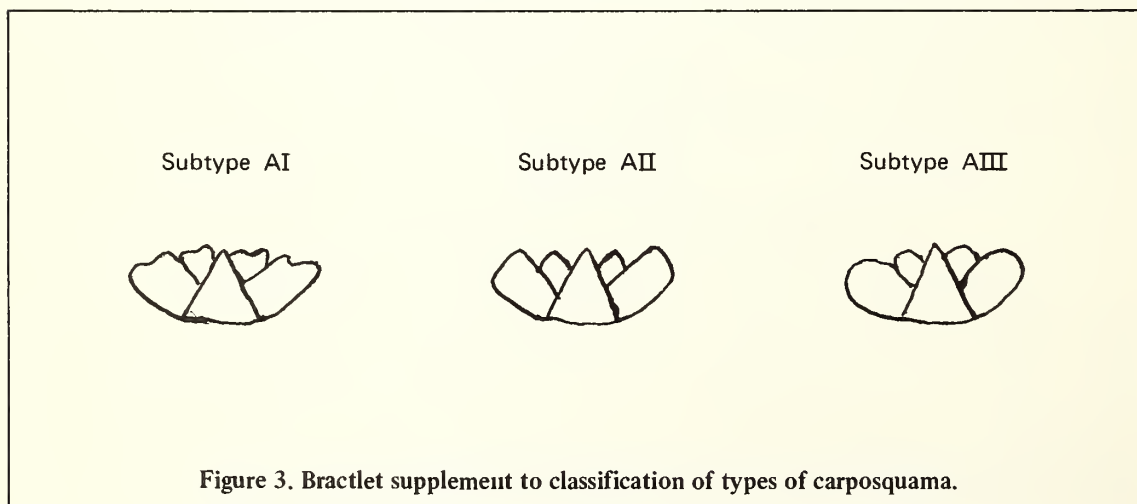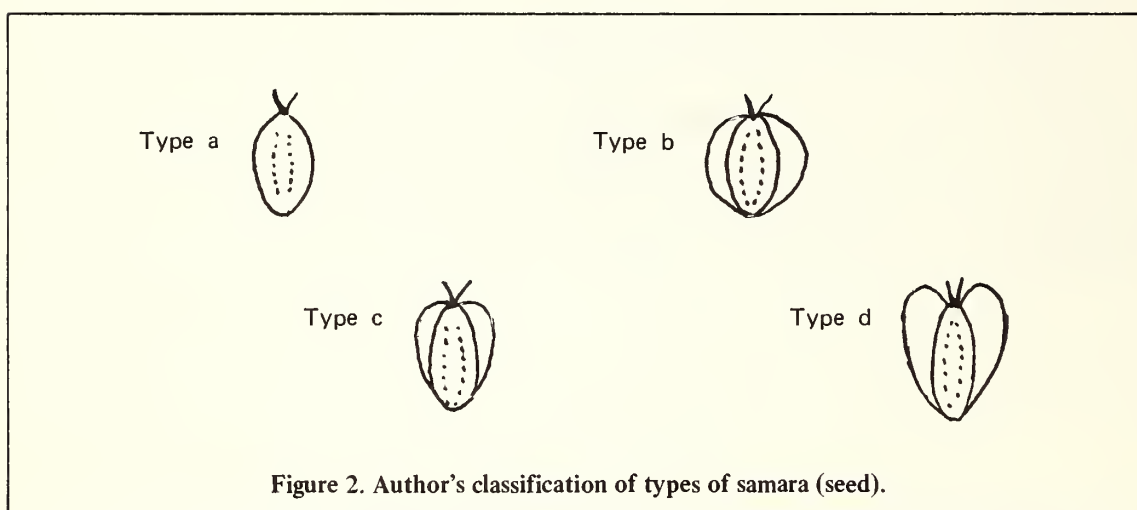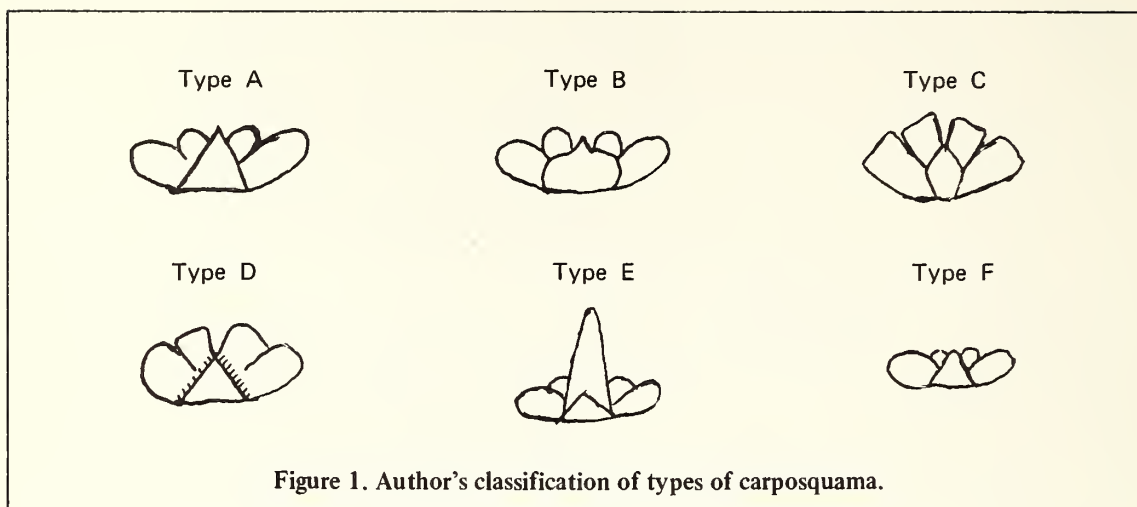
from the middle of Japan proper and reaches Kurile and Saghalen and also extends separately from northern Korea to reach the Amur River on the west side of the Pacific. Although it has no direct relation to the present studies, subspecies *crispa* exists north of our districts (where both other subspecies exist) and extends from southern Greenland, through Labrador, northern North America, inland Alaska, Bering Strait, the whole of Siberia, to reach European Russia. Subspecies *crispa* also extends southward to Korea in East Asia. Hulten (1944) also reported that it grows in the northwestern United States.

It appears that subspecies *maximowiczii,* extending from the south, and subspecies *sinuata* are crossed, and hybrids appear in complicated fashion in Kamchatka. Komarov (1936) regarded the hybrid "species" as *A. kamschatica* (Call.) Kom. (1936) enbloc, since both subspecies are crossed and appear in various forms. There is some question as to whether all the subspecies in a district are regarded as crossed. However, the author approves this since, if parents and hybrids are crossed with each other for many years, it becomes difficult to separate them from each other. Consequently, it is decided to treat this as *A. crispa,* subspecies *kamschatica* (Call.) Murai (of. VI) = *A. crispa-sinuata* x *A. crispa-maximowiczii.* The other mutually crossed subspecies is treated as *A. crispa,* subspecies *mandshurica* (Call.) Hara = *A. crispa-crispa* x *A. crispa-maximowiczii* (cf. VI). The author regards this also as a regional hybrid subspecies. *A. crispa-crispa* x *A. crispa-sinuata* described by Hulten (1944) in the inland of Alaska is treated as *A. crispa,* subspecies *hulteni,* Murai (cf. VI).

TABLE 3.   Division of related species by type of carposquama and samara

Type	Japan		Northwestern United States		Other United States		Europe	
F-d	*A.*	*crispa-maximow.*	*A.*	*crispa-sinuata*	*A.*	*crispa-crispa*	*A.*	*viridis*
AI-a	*A.*	*matsumurae*		—		—		—
AII-b	*A.*	*inokumae*	*A.*	*tenuifolia*	*A.*	*rugosa*		—
AIII-b	*A.*	*hirsuta*	*A.*	*rhombifolia*	*A.*	*serrulata*	*A.*	*glutinosa*
			A.	*rubra*	*A.*	*oblongifolia*	*A.*	*incana*

In summary, it is concluded that subspecies *crispa, sinuata,* and *maximowiczii,* three subspecies of *A. crispa,* appear in the northern Pacific, and mutually crossed subspecies between them appear regionally in various spots. In some districts, such crossing is not observed. In addition, *A. viridis* makes a limited appearance in the European Alps district.

The distribution maps in Figures 5 through 7 are of species belonging to section *Glutinosae.* In general, a smaller, more limited range is believed to
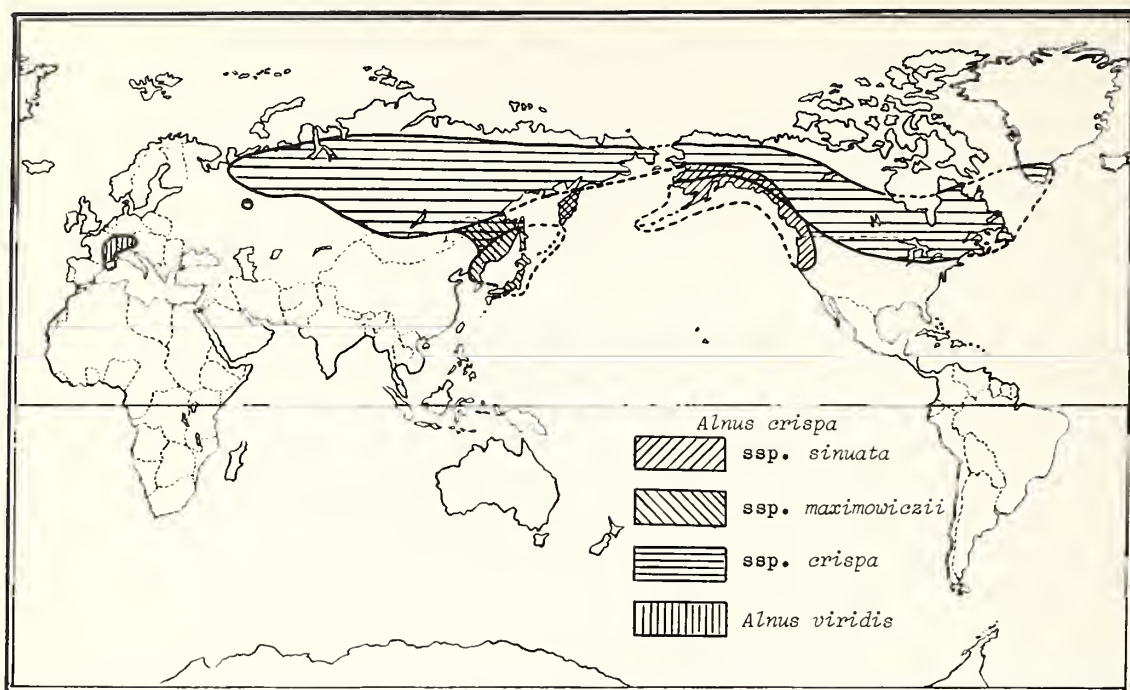
Figure 4. Distribution map of type F-d of section *Alnobetula.*

indicate the alder species' time of prevalence was in a past geologic period, and it has since failed to survive except in a very limited area. The larger, more widespread range indicates the species is more suited to present world climate and consequently it is prevailing at present. Distribution of type AI-a is shown in Figure 5. Only *A. matsumurae* (Murai, 1963) belongs to this type, and it is very limited in distribution, being found only in the subalpine region of middle Japan. Following the criteria stated earlier, this species is apparently the most ancient in section *Glutinosae.*

The three species (Table 3) of type AII-b are distributed as shown in Figure 6, two relating to our districts. On the east side of the Pacific, *A. tenuifolia* is found extending from the west slope of the Rocky Mountains to southern Alaska by way of western British Columbia. On the west side of the Pacific, *A. inokumae* is found in Japan. In particular, *A. inokumae* (Murai, 1962) extends from the southern end of Hokkaido through northern Japan to reach Shizuoka and Gifu Prefectures in the middle of Japan proper, being generally distributed in two groups, northern and central Japan. *A. rugosa* is found in central and northeast North America and, therefore, has no relation to our districts.

An anatomical problem lies in this type AII-b. Chiba (1962) studied chromosome numbers of *A. inokumae* and reported 2n = 14. *Alnus* was previously known to have 2n = 28; however, from this discovery it was clear that 4n = 28. Since those having smaller numbers of chromosomes are primitive, the time of genesis of *A. inokumae* is obviously ancient. Both *A. tenuifolia* and *A. rugosa* have been found to have 2n = 28 (Gram, 1942; Darlington,
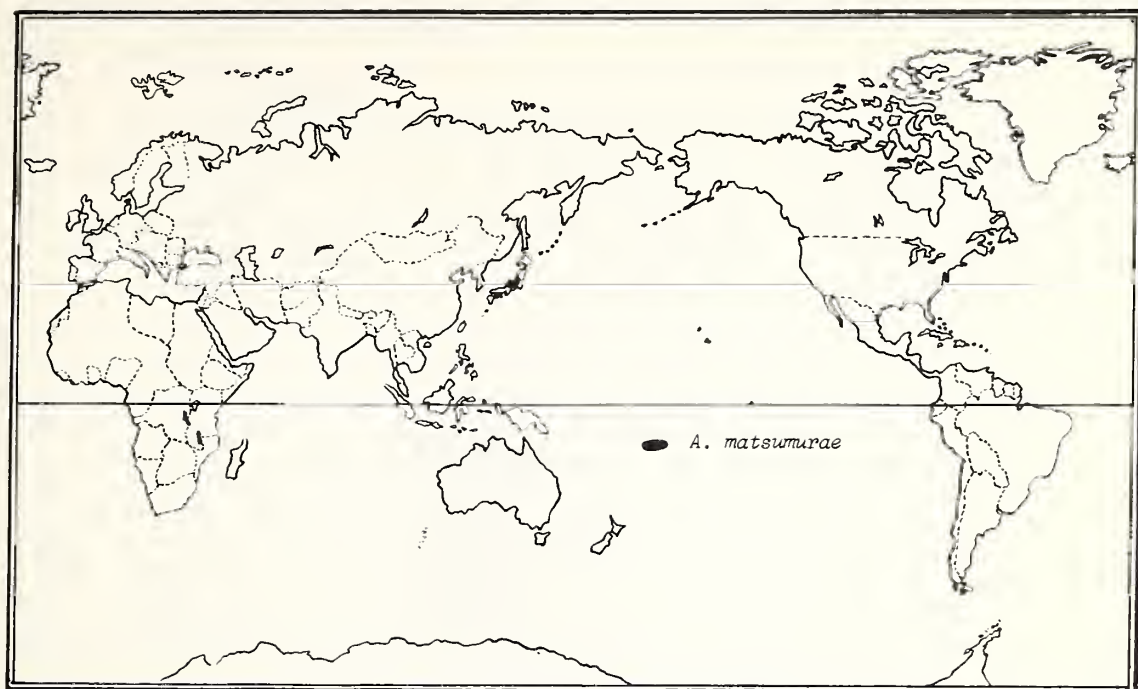
Figure 5. Distribution map of type AI-a.

Legend on map: *A. matsumurae*

Figure 6. Distribution map of type AII-b.

Legend on map:
Alnus tenuifolia
A. inokumae
A. rugosa
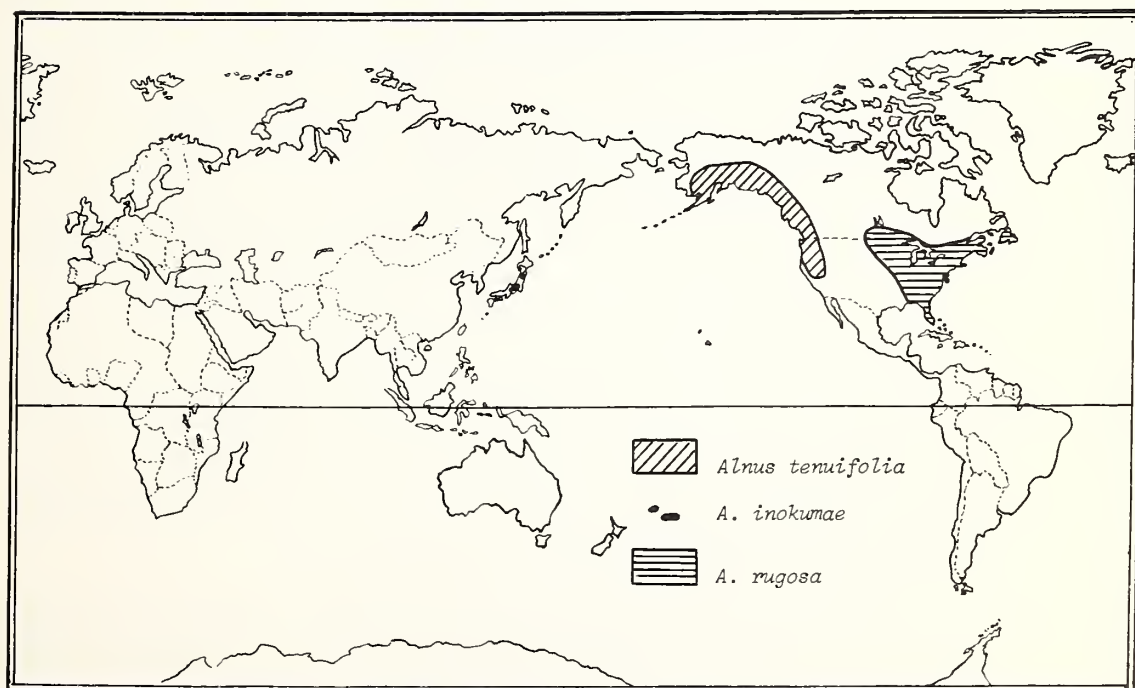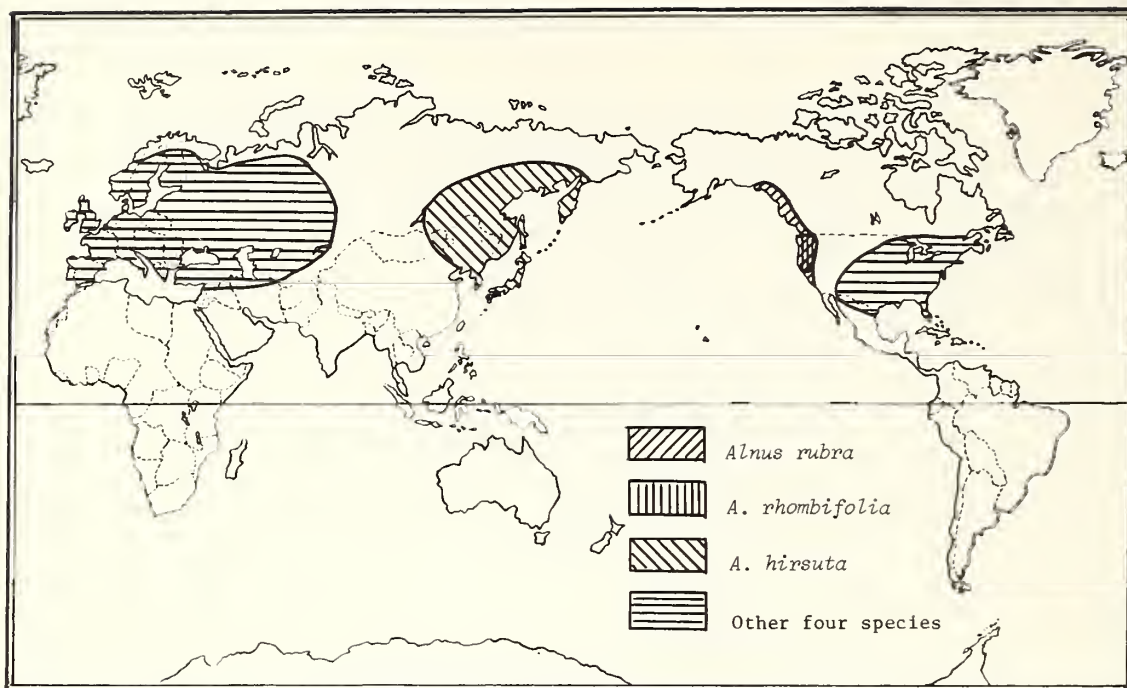
Figure 7. Distribution map of type AIII-b.

1955); on the other hand, the author believes that there is some possibility that individuals having 2n = 14 will be discovered. In summary, it is clear that three species belonging to this type AII-b have independent ranges and do not come in contact with each other; particularly, *A. tenuifolia* and *A. inokumae* are distributed on opposite sides of the Pacific.

Figure 7 shows the distribution of type AIII-b and to which six or seven species belong. Although *A. oblongifolia* is not known to him as yet, the author temporarily assumes that seven species belong to this type. Of species having a relation to our districts, two, *A. rubra* and *A. rhombifolia,* are on the east side and *A. hirsuta* is on the west side of the Pacific, totaling only three species. Separate, *A. glutinosa* and *A. incana* are distributed in West Asia to Europe, and *A. serrulata* and *A. oblongifolia* are in other parts of North America. Although two or three other species' names are given to *A. hirsuta* on the west side, the author (Murai, 1962; Murai, 1963) approves only one species name and two varieties. *A. hirsuta* is widely distributed and seems to extend over Kamchatka, Japan, Baikal, and Yakutsk. *A. rubra* on the east coast extends from California to Idaho and further through British Columbia to southeast Alaska. Only *A. rhombifolia* has a limited distribution area — between Washington, Idaho and California.

In summary, seven species belonging to type AIII-b extend over temperate and subfrigid zones in the northern hemisphere and can be divided into three districts, Europe, East Asia and North America. *A. hirsuta* has the widest distribution, *A. rubra* has an intermediate area, and *A. rhombifolia* has the

most limited area of distribution. Both *A. rubra* and *A. rhombifolia* occur on the west slope of the Rocky Mountains.

DISCUSSION AND CONCLUSIONS

Each of our two districts has four related species as shown in Table 3. The author (Murai, 1965) has constantly attempted to consider the phylogeny of individual sections from the shape and distribution type of genital organs in genus *Alnus* and in this paper considers these with respect to species related to our districts. In the first place, when considering distribution type, it is interpreted (1) that species with limited distribution have the most ancient genesis and, even if it had thereafter a prevailing period, it has since declined to relict status at present; (2) that species relatively widely distributed but divided into discontinuous small isolated groups have a less ancient genesis than the former, went through a prevailing period, and have only begun to decline at present; and (3) that species widely distributed and broadly adapted to habitats have recent genesis and prevail at present because of adaptation to the existing climate. The allied species classified into these types of distribution is summarized in Table 4 with those belonging to the allied section but not found in our districts shown in brackets. It is apparent that only a single species, *A. matsumurae,* belongs to the limited type of distribution; two, *A. inokumae* and *A. rhombifolia* (as well as two others, totaling four) belong to the discontinuous type of distribution; and four, *A. crispa (-sinuata, -maximowiczii), A. tenuifolia, A. hirsuta* and *A. rubra* (as well as four other species, totaling eight), belong to the wide type of distribution.

TABLE 4.   Related *Alnus* species classified by distribution types

I.   Limited-distribution type

   A.   matsumurae

II.   Intermittent-distribution type

   A.   inokumae,   A.   rhombifolia,

   (A.   viridis),   (A. oblongifolia)

III.   Wide-distribution type

   A.   crispa-sinuata,   A.   crispa-maximowiczii,

   A.   tenuifolia,   A.   rubra,   A.   hirsuta,

   (A.   crispa-crispa),   (A.   rugosa),

   (A.   serrulata),   (A.   glutinosa),   (A.   incana)

Before considering phylogeny, one must judge whether a living species is thriving or declining. The number of departments (branches) of species belonging to each section can be used to judge. Where a species has a larger number of departments, it is considered thriving; and where it has a smaller number of departments, it is believed declining. It is further interpreted that species having a larger distribution area at present are thriving, and those having a smaller distribution area at present are declining. That is, those having a larger number of departments and a wider distribution area are thriving, and those having smaller number of departments and narrower distribution area are declining.

Section *Alnobetula* is problematic in these interpretations. Since only two species are believed to belong to this section, section *Alnobetula* cannot be regarded as thriving due to number of species; however, if the number of subspecies is taken into consideration, the two species and five subspecies now approved allows us to consider section *Alnobetula* thriving. If its distribution is taken into consideration, it is found to be widely and continuously distributed around the North Pole and can, therefore, also be interpreted as a thriving section, which is less problematic. Perhaps those taxons, which have developed only to subspecies at present, will thereafter develop further, possibly to species, since they are widely distributed.

Taking into account the previous description of thriftiness or decline of section or species and determining that distinctive shapes of genital organs are found in thriving sections and species and in declining ones, the author has evolved the following phylogeny for these organs. In type of carposquama, Figures 1 and 3 have been combined into Figure 8, where (1) the primitive type lies at the bottom, (2) evolution lies on the ordinate, (3) period lies on the abscissa, and (4) species prevailing at present are shown by **O** and those only surviving at present are shown by O. Type E is regarded as primitive, type A is regarded as the most evolved, and among type A, subtype AIII is regarded as the most eminent. In phylogeny of samara type, Figure 9 is similarly derived from Figure 2.

Table 5 is constructed by combining both Figures 8 and 9 and relating them to the sections devised by the author. It is apparent that if species where both type of carposquama and samara are prevalent are in the prevailing sections, prevailing sections will include three; i.e., section *Alnobetula* and the greater portions of section *Japonicae* and section *Glutinosae*. If species with primitive types of both carposquama and samara are in surviving sections, surviving sections will include section *Cremastogyne* and section *Fauriae*. If species where both are mixed with each other are in intermediate sections, they will include two, section *Bifurcatus* and section *Clethropsis* plus portions of section *Japonicae* and section *Glutinosae*. It is believed that this shows the apparent relation between prevalence and survival (relic) and relation of phylogeny in sections. Considering the above, one can interpret that both type F-d and type AIII-b include many species prevailing at present and type AI-a and type AII-b include many species which have declined (Table 3).
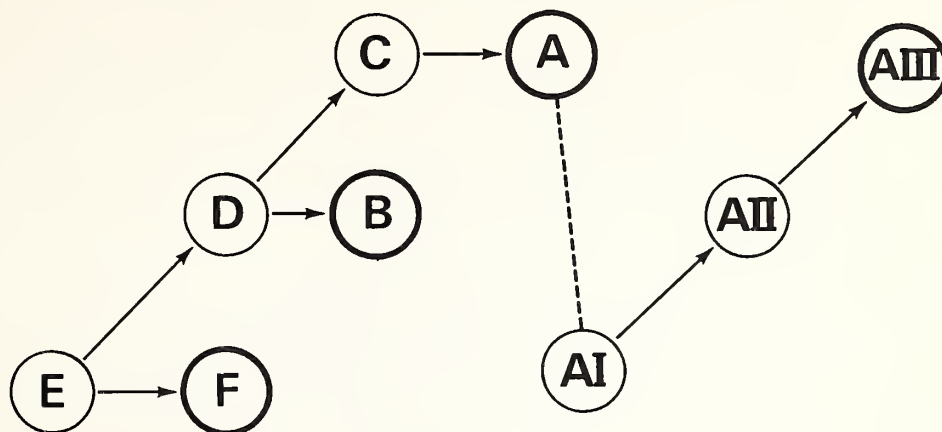
Figure 8. Phylogeny of types of carposquama.
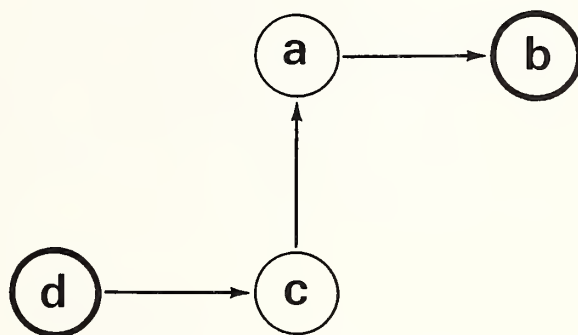
Figure 9. Phylogeny of types of samara.

The gradient from declining — surviving species to prevailing — widely spread species can be arranged in four stages as follows:

First stage — *A. matsumurae*
Second stage — *A. inokumae*
Third stage — *A. tenuifolia, A. rhombifolia,*
(*A. rugosa*), (*A. viridis*), and (*A. oblongifolia*)
Fourth stage — *A. crispa-sinuata, A. crispa-maximowiczii,*
A. rubra, A. hirsuta, (*A. crispa-crispa*),
(*A. serrulata*), (*A. glutinosa*), and (*A. incana*)

Since *A. matsumurae* (first stage) shows limited distribution (Table 4) and has type AI-a (Table 3), it is the most primitive and has the most ancient genesis. Since *A. inokumae* (second stage) has a discontinuous distribution type (Table 4) and type AII-b (Table 3), it is the second most primitive, and its genesis is still considerably ancient. Two species, *A. tenuifolia* and *A.*

rhombifolia, plus three other species (third stage) are included in the discontinuous distribution type or belong to type AII-b or to those undecided as to classification. Since three subspecies of *A. crispa, A. rubra, A. hirsuta,* and three other species (fourth stage) have a wide distribution type (Table 4) and belong to type F-d or type AIII-b (Table 3), they are best adapted to the present climate, and their genesis is the most recent. The five species in the third stage are placed between a species in the second stage and six in the fourth, and their genesis is believed older than that of those in the fourth stage.

These phylogenetic relationships are illustrated for species on both sides of the Pacific in Figure 10. Species with older genesis are placed below and those with more recent genesis above; they are connected with each other by arrows (———▶) according to the above-mentioned stages. It is interpreted that alders in our districts originated first as *A. matsumurae* (first stage) on the west side of the Pacific, then developed into *A. inokumae* (second stage), and thereafter went over to the east side to give rise to *A. tenuifolia* and *A. rhombifolia* in the third stage. On the east side, *A. rubra* later developed (fourth stage). Since species belonging to the third stage are still presently unknown on the west side, the author suggests that *A. inokumae* (second stage) continued as *A. inokumae* in the third stage, and thereafter developed into *A. hirsuta* (fourth stage). The author believes that correctness of this construction will surely be proved in the future by studies on karyotype, etc.

Alnus crispa probably originated in the Tertiary glacial epoch, and the author assumes that it originated in Japan or in northern Pacific.

Figure 10. **Phylogenetic development of related species on both sides of the Pacific.**
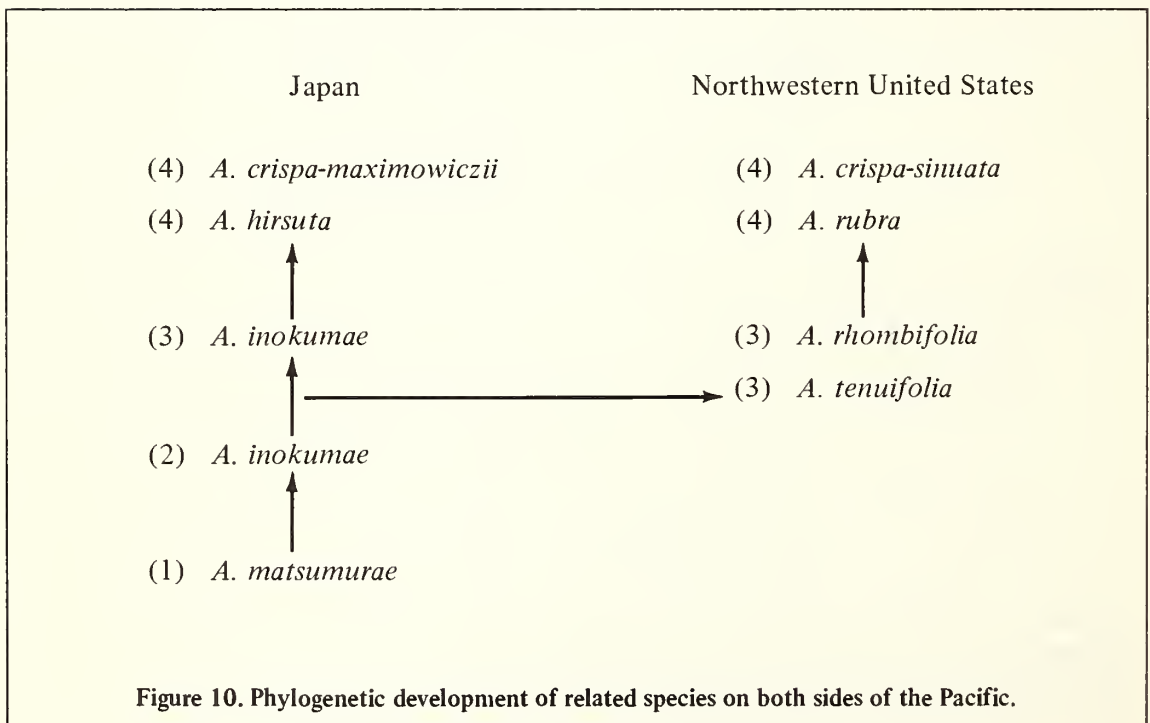
ARRANGEMENT OF NEW SUBSPECIES OF NATURAL HYBRIDS

1. *Alnus crispa* (AITON) PURSH
   x subsp. *kamschatica* (CALLIER) MURAI comb. nov.
   A. crispa, subspecies *sinuata* x *A. crispa,* subspecies *maximowiczii* MURAI
   Syn. *A. sitchensis,* var. *kamschatica* CALL. ex. SCHNEID., Ill. Handb.
       Laubh. I. 123 (1904)
   A. fruticosa, var. *kamschatica* (CALL.) KOM., Fl. Pen. Kamtsch.
       1. 47 (1929)
   A. x *kamschatica* (CALL.) KOM., Fl. URSS. V. 310 (1936)
   A. sinuata x *A. maximowiczii* KOM., 1.c. (1936)
   A. fruticosa (non RUPR.) HULT., Fl. Kamtch. II. 34 (1928)
   Nom. *Kamchatikan* green alder
   Distr. *Kamchatka,* Northern Kurile.

2. *Alnus crispa* (AIT.) PURSH
   x subspecies *mandshurica* (CALLIER) HARA, Jour. Fac. Sci. Univ.
       Kokyo III. -6 (2). 32 (1952)
   A. crispa, ssp. *crispa* x *A. crispa,* ssp. *maximowiczii* MURAI
   Syn. *A. fruticosa,* var. *mandshurica* CALL. ex SCHNEID., Ill. Handb.
       Laubh. I. 121 (1904)
   A. mandshurica (CALL.) H.-MAZZ., Oestr. Bot. Zeit. LXXXI. 306 (1932)
   A. vermicularis NAKAI, Bot. Mag. Kokyo XXXIII. 46 (1919)
   A. gigantea NAKAI, Jour. Jap. Bot. XVI. -2. 67 (1940)
   Nom. Manchurian green alder
   Distr. Eastern Asia: Amur, Ussuri, Northeast Manchuria, Northern
       Korea, Saghalin.

3. *Alnus crispa* (AIT.) PURSH
   x subspecies *hulteni* MURAI nom. nov.
   A. crispa, subspecies *crispa* x *A. crispa,* subspecies *sinuata* HULTEN
       Lund. Univ. Arsskr. N.F. Avd. 2, XL. -1. 588. pl.-447b (1944)

The description of HULTEN as follows:

In Alaska, along the southern coast, *Alnus crispa,* subspecies *sinuata,* is found which has large, thin broadly ovate, acute, more or less sinuate, sharply serrulated leaves, whereas *A. crispa,* subspecies *crispa,* found in the central and northern parts has smaller, thicker, narrower, more abruptly pointed, not sinuate, sharply serrulated leaves. To draw a sharp line of demarcation between these two subspecies is, however, impossible. Forms that are more or less intermediate between them are not infrequent although sinuate leaved specimens are increasingly rare towards the north, and non-sinuate specimens are lacking in the extreme coastal belt.

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Comparison of vegetation in adjacent alder, conifer, and mixed alder-conifer communities. I. Understory vegetation and stand structure

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Abstract

Vegetational analyses of adjacent 40-year-old coastal Oregon stands of red alder, conifers, and mixed alder-conifer showed marked differences in coverage and richness of understory. Shrubby species were confined mainly to the pure alder stand, where they formed a dense layer. Herbaceous plants were best developed in the alder and mixed stands and ground-dwelling cryptogams in the mixed and conifer stands. Differences in canopy density and, perhaps, in nutrition probably accounted for most of the contrasts. Although current regeneration of trees was uniformly absent, supressed Sitka spruce saplings persisting in the alder and mixed stands could, by responding to future release, partially replace a deteriorating alder overstory.

A variety of biological studies are being conducted in three adjacent 40-year-old stands of red alder (*Alnus rubra*), conifer (mainly Douglas-fir (*Pseudotsuga menziesii*)), and mixed alder and conifer growing on the Oregon coast (Berntsen, 1961; Franklin et al., 1968; Bollen and Lu, 1968; and Lu, Chen, and Bollen, 1968). A quantitative vegetational analysis of these stands was deemed not only interesting in itself but was also needed as an aid in interpretation of other studies.

In the spring of 1966 we made such an analysis. Our data on stand structure and composition of the understory vegetation, including ground-dwelling cryptogams, are presented in this paper. Data on epiphytic, epixylic, and epilithic cryptogams are presented elsewhere (Pechanec and Franklin, 1968).

ENVIRONMENT

The stands studied are located in the Cascade Head Experimental Forest about 2 miles north of Otis, Oregon. They lie within the mild, wet coastal

climatic zone sometimes called the "fog belt" (Madison, 1957). Average annual rainfall in the study area is between 90 and 100 inches, and temperatures below freezing or in excess of 80 F are uncommon. The stands occupy a relatively uniform, gentle (about 15 percent) southwesterly facing slope about 6 miles from the ocean. Soils are deep Astoria-like Sols Bruns Acides which have been fully described by Franklin et al. (1968). All are moderately fine textured and derived from deeply weathered Eocene siltstone.

HISTORY OF STANDS

The 40-year-old stands occupy a site which was once cleared for agriculture but was abandoned about 1925. A well-stocked stand of alder and conifer reproduction developed. Between 1935 and 1937, three long-term silvicultural study plots, which constitute the three stands employed in the present study, were established. On one 1-acre plot, all conifers were removed and the remaining alders thinned to a spacing of 8 by 8 feet, leaving 733 trees per acre. On another 1/2-acre plot, all alders were removed and conifers were thinned to 1,148 trees per acre. A third 1-acre plot containing about 3,000 trees per acre, of which 40 percent were alder and 60 percent conifer, was left untouched. Berntsen (1961) described the subsequent development of the stands up to 1957. The three plots constitute our alder, conifer, and mixed stands.

Methods

A 15- by 25-meter macroplot in the center of each stand was used to obtain data on understory vegetation and forest structure and composition. Each macroplot was outlined on the ground with cloth tapes, the long axis across the slope. Each macroplot was then divided into three 5- by 25-meter segments with two more tapes. Frequency and coverage of all shrubs, herbs, and ground mosses and liverworts were determined on fifty 20- by 50-cm plots systematically placed at 1-meter intervals along the inside boundaries of the center 5- by 25-meter segment. Daubenmire's (1959) procedures for estimating and calculating canopy coverage were used. The remainder of the macroplot and stand was examined for additional species.

All trees on each macroplot were tallied by species and size class.

Results

Understory Community

Understory vegetation was much better developed under pure red alder than under conifer, with the mixed stand intermediate (Table 1). A total of 40 species of shrubs, herbs, and ground cryptogams were recorded — 36 in the alder stand, 23 in the mixed stand, and 19 in the conifer stand. Sixteen of the 40 species were observed in only one of the three stands, 13 of these 16 occurring only under pure alder; most were minor components, however.

Coverage by the different understory layers differed dramatically. The alder stand was the only one with a significant coverage by the shrub layer,

mostly of *Sambucus melanocarpa* and *Rubus spectabilis* (Table 1). Only 2 percent and a trace of shrub coverage were recorded in the mixed and conifer stands, respectively. The alder and mixed stands had comparable coverage within the herb layer, but the conifer stand herb coverage was again significantly lower, having less than half as much. Coverage by ground cryptogams was considerably higher in the conifer and mixed stands than in the pure alder stand; proportionately high coverage of *Eurhynchium oreganum* accounted for most of this difference.

Most of the important herbs occurred in all three stands although there were some shifts in dominance (Table 1). *Maianthemum bifolium* and *Polystichum munitum* were consistently important. On the other hand, *Montia sibirica,* which had high frequency and coverage in the pure alder and mixed stands, was nearly absent from the conifer stand. *Stachys mexicana* was the only major herbaceous species confined to a single stand condition, pure alder.

Stand Structure

Regeneration of tree species was not yet taking place in significant numbers (Table 2). A very few western hemlock seedlings (<3 feet tall) were

TABLE 1.—Frequency and canopy cover of understory species in adjacent red alder, conifer, and mixed alder-conifer stands based on 50 systematically placed 20- by 50-cm plots in each stand.[1]

Layer and species	Alder		Mixed		Conifer	
	Freq.	Cover	Freq.	Cover	Freq.	Cover
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Shrub layer:						
Rubus spectabilis	80	58	4	2		
Sambucus melanocarpa	52	43	2	< .5		
Rubus parviflorus	10	4				
Acer circinatum	10	9		+		+
Holodiscus discolor	2	1				
Menziesia ferruginea		+				+
Vaccinium parvifolium		+		+		+
Sum of coverage by species in shrub layer		115		2		
Herb layer:						
Maianthemum bifolium	98	24	70	38	82	19
Montia sibirica	94	37	82	42		+
Polystichum munitum	26	14	24	14	20	11
Rubus ursinus	22	3	10	1	8	< .5

Table 1.—Frequency and canopy cover of understory species. . . (Continued)

Layer and species	Alder		Mixed		Conifer	
	Freq.	Cover	Freq.	Cover	Freq.	Cover
	Number	Percent	Number	Percent	Number	Percent
Disporum smithii	16	3	6	1	10	< .5
Pteridium aquilinum	4	2	2	1	2	2
Carex leptopoda	4	2	2	< .5		+
Trillium ovatum	4	1		+	6	1
Galium triflorum		+	2	< .5	4	1
Luzula parviflora		+		+	2	1
Trisetum cernuum	4	1		+		
Stachys mexicana	28	6				
Viola sempervirens			2	< .5	4	< .5
Oxalis oregana		+				+
Osmorhiza chilensis	2	< .5				
Melica subulata	2			+		
Dryopteris spinulosa dilatata		+		+		
Athyrium filixfemina		+		+		
Poa marcida		+				
Streptopus amplexifolius		+				
Polypodium vulgare		+				
Tiarella trifoliata						+
Sum of coverage by species in herb layer		93		97		35
Moss layer:						
Eurhynchium oreganum	56	8	98	54	100	55
Isothecium spiculiferum	10	< .5	18	1	6	< .5
Eurhynchium stokesii	60	4	2	< .5		
Mnium insigne	16	1				
Plagiothecium denticulatum	14	1				
Rhytidiadelphus loreus	12	1				
Plagiothecium undulatum	8	< .5				
Campylium sp.	4	< .5				
Mnium punctatum	2	< .5				
Neckera			2	< .5		
Scapania bolanderi					2	< .5
Sum of coverage by mosses and liverworts		15		55		55
Sum of coverage, all understory species		223		154		90

[1] A "+" indicates that the species was present in the stand but was not observed on a plot.

found in the conifer stand; no seedlings of any tree species were found in the other stands. A number of suppressed Sitka spruce saplings (>3 feet tall and <4 inches dbh) were found in the alder and mixed stands. A check of comparable saplings growing just outside plot boundaries revealed most of these had persisted since establishment 25 to 35 years earlier.

Discussion

The relative richness of understory vegetation under stands of alder has frequently been noted. For example, Sharpe[1] found red alder stands on alluvial sites on the Olympic Peninsula had a greater abundance of herbs, grasses, grasslike plants, and ground cryptogams than most conifer stands. Smirnova and Sorogovets (1966) contrasted the abundance of herbs in *Alnus incana* stands with conditions under stands of aspen and birch growing on similar sites. They also mention that herbage is reduced under an admixture of *Picea excelsa* and suggest alder preservation for improvement of herbage quality.

Why was the understory more lush under pure alder and mixed stands than under the pure conifer stand at Cascade Head? We suggest that this primarily reflected greater amounts of light passing through the more open and season-

[1] *Sharpe, Grant William. A taxonomical-ecological study of the vegetation by habitats in eight forest types of the Olympic rain forest, Olympic National Park, Washington. 335 p. 1956. Ph.D. thesis on file at Univ. Wash.*

TABLE 2.—Stand structure in adjacent 40-year-old red alder, conifer, and mixed alder-conifer stands.[1]

Stand and species	Diameter at breast height							
	<2 in.		2-4 in.	4-8 in.	8-12 in.	12-16 in.	16-20 in.	20-24 in.
	<3 ft. tall	>3 ft. tall						
	- *Number of trees* -							
Red alder stand:								
Red alder			1	10	17	2		
Sitka spruce		6	8					
Mixed stand:								
Red alder			2	7	11	3		
Sitka spruce		14	23	15				
Douglas-fir				1	6	5	1	
Conifer stand:								
Douglas-fir				1	2	9	5	2
Western hemlock	8	2		2	1			
Sitka spruce			2	1				
Red alder				1				

[1]Tally of trees on 15- by 25-m macroplot in the middle of each stand.

ally leafless alder canopy. Many shrub and herb species abundant in the alder stand are known to be relatively intolerant, light-demanding species, e.g., *Rubus spectabilis*. Also, as Vézina and Grandtner (1965) have shown, species of herbs may leaf out and flower or even complete their entire life cycle prior to development of a deciduous tree canopy in the spring. Several species present at Cascade Head were well along in development prior to red alder bud burst, *Montia sibirica* being a notable example. Higher nitrogen content of the soil under red alder (Franklin et al., 1968) may also promote greater development of understory vegetation. Some Russians have emphasized this factor (Gel'tman and Parfenov, 1966).

Lower coverage of cryptogams under the alder stand probably resulted from low light levels under the dense herb and shrub layers as well as greater quantities of smothering broad-leaved litter. Low-lying ground mosses and liverworts were not well adapted to meet competition of this type. Ground cryptogams did best in the conifer stand where competing vascular understory plants were largely absent.

No successional trends in tree species were evident after 40 years, as neither alder nor conifers were reproducing. Relative sizes of red alder and Douglas-fir in the mixed stand suggest alder was beginning to drop behind in the growth race. Since red alder is a relatively short-lived species (Fowells, 1965), the Douglas-firs, now occupying a dominant crown position, will take over more and more growing space.

Some suppressed Sitka spruce saplings were present in the mixed and pure alder stands. It appears many of these will persist until the alder overstory breaks up. If they then respond to release, an understocked stand of Sitka spruce could be expected to succeed the alder. Sitka spruce regeneration has commonly been observed in other stands of red alder in the fog belt region along the Oregon coast. Sitka spruce forest is known to succeed thickets of *Alnus sinuata* in coastal Alaska (Cooper, 1931). Gel'tman and Parfenov (1966) have described successional replacement of *Alnus incana* stands by those of spruce in Belorussia beginning, in many cases, with simultaneous establishment of alder and spruce and involving extended periods of spruce suppression by alder.

We have observed regeneration of western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) growing in red alder stands elsewhere in the region, particularly in western Washington. Since both are relatively tolerant species, a successional sequence similar to that suggested for alder stands with Sitka spruce might be expected.

The successional sequence proposed here differs somewhat from that described for other western Oregon red alder stands by Newton, El Hassan, and Zavitkovski (1968). In most of their stands, seedlings and saplings of all tree species were absent from the understory; Douglas-firs suppressed in early stages of stand development did not persist. They suggest that alder stands of this type deteriorate into nonforested areas of brush species, such as salmonberry, which are only slowly reclaimed by conifers.

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On the ecology
of Sitka alder
in the subalpine zone
of south-central Alaska

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Abstract

*Alder serves as an important colonizer in priseres on deglaciated terrain, river bottom lands, and rocky and gravelly hillsides in Alaska. It also is a significant factor in secondary succession on many mechanically disturbed sites and burned-over sites in forested areas of south-central Alaska. Less well known is its role as an enduring, dominant component of a well-developed vegetational zone above timberline. Small to extensive stands of Sitka alder (*Alnus crispa *ssp.* sinuata*) and a mosaic of tall-growing grass and forb communities characterize a Subalpine Zone of glaciated uplands and moist mountain valleys in south-central Alaska. The alder occurs on steep rocky slopes to level terrain with relatively deep soils. Nitrogen contents of soil generated under alder are some of the highest recorded for Alaska. These soils also are some of the most acidic with pH values as low as 3.3. The associated native herb communities acquire considerable growth at a rapid rate, which is being utilized in some areas by a fledgling beef industry. But much research is needed to learn how best to exploit the productive potential of this zone.*

Introduction

Alder has figured prominently in the vegetational history of south-central Alaska, both prior to the Pleistocene and in postglacial times (Bowman, 1934; Heusser, 1965; Wolfe, Hopkins, and Leopold, 1966; Wolfe, 1966). Today Sitka alder (*Alnus crispa* ssp. *sinuata* (Regel) Hult.) is an important colonizer, building the nitrogen content and organic matter of soils on recently deglaciated terrain of coastal regions (Crocker and Major, 1955; Crocker and Dickson, 1957; Lawrence, 1958). It may be absent, however, from similar terrain on more inland sites (Viereck, 1966). It also colonizes streamsides and sites deforested by fires (Lutz, 1956; Heilman, 1966) and other agencies. Previous studies have emphasized these colonizing roles of alder that lead to the establishment of more mature wooded stands.

This paper concerns a more enduring role of Sitka alder in the vegetation of Alaska. Hultén (1937), possibly, was the first to refer to an Alaskan

Subalpine Zone containing alder in a discussion of the vegetation of the Aleutian Islands. He described a poorly developed manifestation of the zone on Unimak, the easternmost island, and compared it with a similar vegetation zone in eastern Asia across the Bering Sea. This somewhat unique zone is well represented in south-central regions bordering the Gulf of Alaska and inland to the upper Cook Inlet region and Susitna Valley (Fig. 1). The zone includes alder, tall grass, and forbs as dominants and develops some distinctive soil characteristics. It is involved in agriculture and wildlife management.

Observations for this paper were made principally in the Cook Inlet region. The more detailed information was obtained on mountain slopes above the lower Matanuska Valley, particularly in the Little Susitna drainage north of Palmer. Other references to and treatments of the vegetation of this zone in the south-central region may be found in Cahalane (1959), Hanson (1951), Heusser (1957, 1965), Mitchell (1966), Piper (1905), and Rieger and Wunderlich (1960).
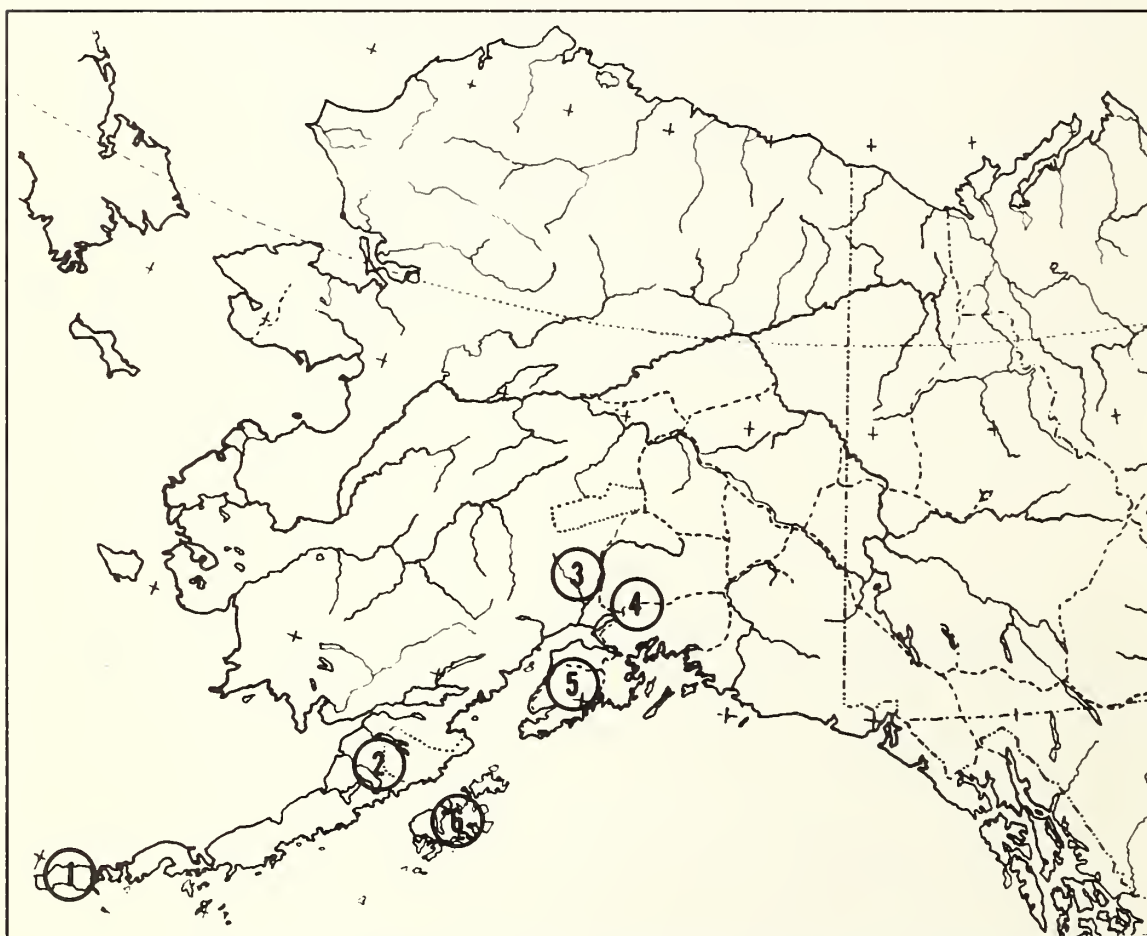
Figure 1. The encircled numbers denote geographic locations in the south-central Alaska region mentioned in the text: 1, Unimak, easternmost Aleutian Island; 2, Alaska Peninsula; 3, Susitna Valley; 4, lower Matanuska Valley; 5, Kenai Peninsula; 6, Kodiak Island.

Findings

FLORISTICS AND VEGETATIONAL ASPECTS OF SUBALPINE ZONE

Timberline rises in the lower Matanuska Valley from about 460 m to 625 m in elevation; its lower levels are found in the more moist valleys. Very steep, relatively moist slopes above timberline are often densely clothed with Sitka alder (Fig. 2) whereas more moderate slopes generally support a mixture of alder and herbaceous community types (Fig. 3). The Subalpine Zone may be narrow and fragmentary (Fig. 4) or extend over 400 m in altitude. On drier slopes it is absent or poorly developed. In the Little Susitna Valley, it extends from about 460 m to 850 m in elevation. Outlying alder shrubs have been noted occurring up to 1,025 m in elevation.

The upper limits of the zone frequently correspond with the upper limits of lateral morainal deposits (Figs. 2-4). Talus and other sites above these deposits occasionally support alder thickets. The alder and tall-herb association also establishes on burned-over slopes below timberline and may form a continuous pattern with the subalpine association above.

Figure 2. A steep, northwestward-facing subalpine slope densely invested with Sitka alder in the Little Susitna Valley north of Palmer, Alaska.

Figure 3. A mixture of Sitka alder and herbaceous stands on glacial till and morainal deposits in the Little Susitna Valley. The altitudinal extent of the subalpine association corresponds with that of the lateral morainal deposits marked by the ridges at the upper limits of the zone. Siberian fescue dominates the foreground, fireweed and spiny woodfern the dark area through the center, and bluejoint the light-colored triangular area below the alder thicket.

Intermixed with Sitka alder is a mosaic of herbaceous community types with bluejoint (*Calamagrostis canadensis* (Michx.) Nutt.), fireweed (*Epilobium angustifolium* L.), lady fern (*Athyrium filix-femina* (L.) Roth.), spiny wood-fern (*Dryopteris austriaca* (Jacq.) Woyn.), and Siberian fescue (*Festuca altaica* Trin.) as frequent dominants. All but the last, a bunchgrass, generally grow from 6 to 12 dm and more in height. The shorter growing Siberian fescue occupies drier sites on shallow soils. Tall grass stands of bluejoint develop on the deepest soils of the herbaceous sites. In the more moist coastal region, bluejoint stands are extensive. Farther inland they become fragmentary and often occur adjacent to and downhill from an alder thicket (Fig. 3).

Willows (*Salix* spp.) are the most important of the other woody constitu-ents of this zone. They occasionally abound in creek drainages and on some uplands. The shrubs mountain ash (*Sorbus scopulina* Greene), elderberry (*Sambucus racemosa* L.), spiraea (*Spiraea beauverdiana* Schneid.), American red currant (*Ribes triste* Pallas), devils club (*Oplopanax horridus* (Sm.)

Figure 4. The narrow gray band of alder above the spruce-birch woods delimits a fragmentary subalpine zone on a steep north slope of the Chugach Mountains south of Palmer. The contour ridges in the Subalpine Zone are lateral moraines.

Miguel), highbush cranberry (*Viburnum edule* (Michx.) Raf.) and trailing black currant (*Ribes laxiflorum* Pursh) also occur here. Balsam poplar (*Populus balsamifera* L.) and white spruce (*Picea glauca* (Moench) Voss), or Sitka spruce (*P. sitchensis* (Bong.) Carr.) in the coastal region, often are present.

Alder shrubs generally grow from 3 to 5 m in height in this zone and decidedly procumbent, particularly on the downhill side. Lady fern and spiny woodfern often dominate the densely shaded undergrowth with oak fern (*Gymnocarpium dryopteris* (L.) Newm.), bluejoint, arctagrostis (*Arctagrostis latifolia* (R. Br.) Griseb.), twisted stalk, wood horsetail, and *Rubus pedatus* J. E. Smith commonly present. Occasional shrubby constituents of the undergrowth are devils club, American red currant, trailing black currant, and elder.

Sitka alder is not restricted to any particular type of habitat in this zone. It grows on very steep slopes and on level terrain. It obtains on rocky debris
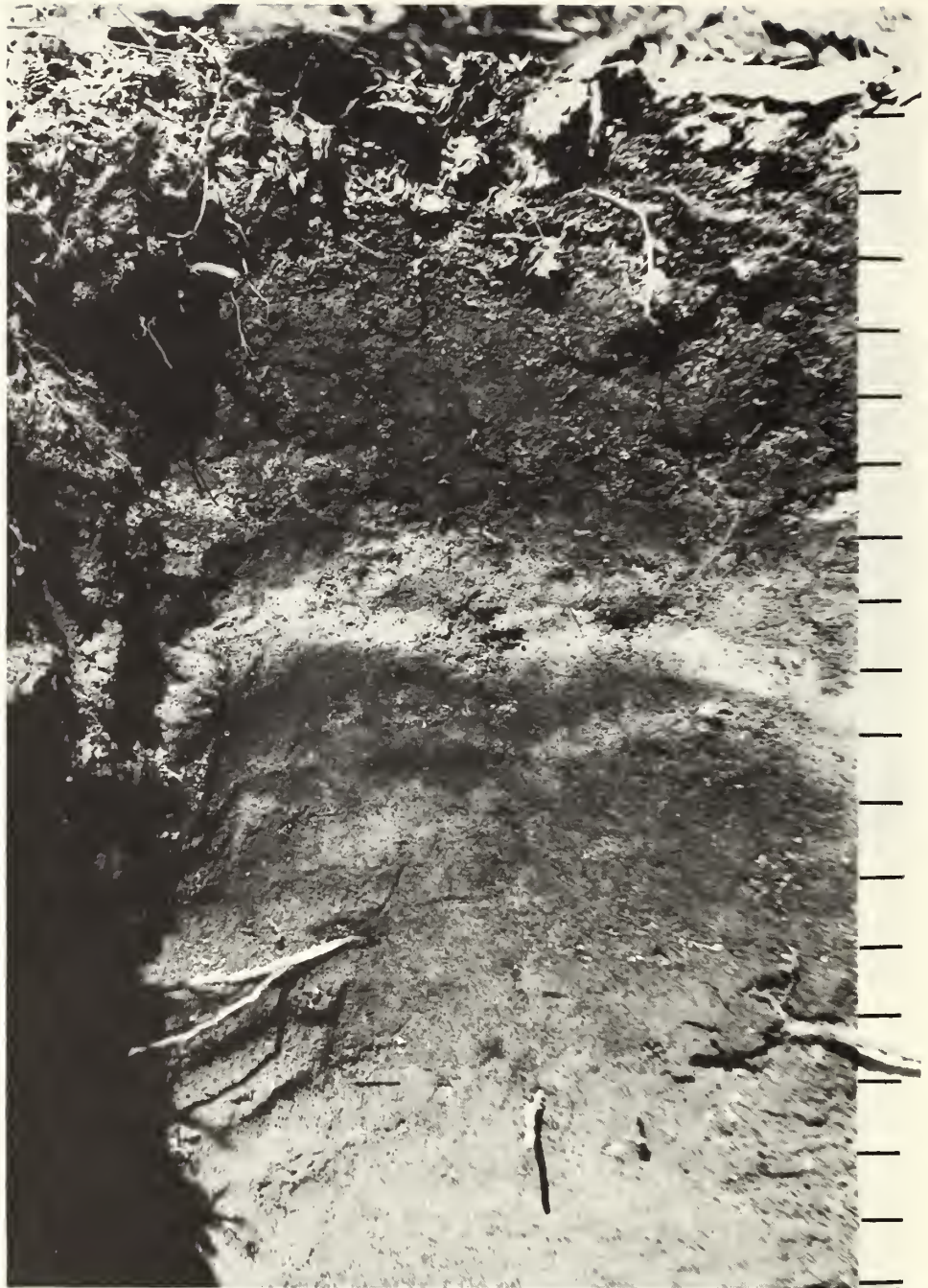
Figure 5. A podzolic soil profile generated under Sitka alder at ca. 550-m elevation in the Subalpine Zone of the Little Susitna Valley. The scale on the right is marked off in inches.

as well as on some of the deepest soils in the zone and frequents all exposures. But where contrasting exposures are differentially occupied by alder and other community types, the alder community generally prevails on the more moist exposure.

SOIL CHARACTERISTICS

The more mature soils occurring under alder in this zone, about 20 inches (50 cm) or more in depth, are podzolic in nature (Fig. 5). The highly humic soils bear a thick, compact layer of litter and raw humus, a dark to black A_1 horizon, a thin ash-gray A_2 horizon, a dark- to reddish-brown iron-laden B horizon, and a yellowish C horizon. They are extremely acidic and high in carbon and nitrogen. Alder soils from both the subalpine belt and burned-over land below timberline were much more acidic and higher in carbon and nitrogen than forested soils sampled in the same region (Table 1). This holds true in general for comparisons with other forest soils of Alaska (Kellogg and Nygard, 1951; Rieger et al., 1959, 1962; Rieger and Wunderlich, 1960; Wilde and Krause, 1960).

TABLE 1. **Properties of soil under Sitka alder compared with that under white spruce-birch woods in lower Matanuska Valley region, Alaska**

Profile and site information	No. of sites	pH[1]	Carbon[2]	Nitrogen[3]	C/N ratio
			- - - - - - *Percent* - - - - - -		
Upper layer (A_1 hor.)					
alder, subalpine	14	3.8	22.7	1.24	18.4
alder, below timberline	6	4.0	27.6	1.47	18.7
mixed woods	2	5.0	9.0	.32	29.5
Intermediate (B hor.)					
alder, subalpine	14	4.6	14.4	.58	25.4
alder, below timberline	6	4.8	14.0	.65	21.7
mixed woods	2	5.6	6.8	.17	41.7
Lower (C hor.)					
alder, subalpine	3	5.2	9.5	.28	34.0

[1] *1:1 H_2O solution.*
[2] *Determined by combustion method.*
[3] *Kjeldahl determination.*

Within the Subalpine Zone, alder soils were more highly acidic and higher in carbon and nitrogen than those of adjacent herbaceous communities (Table 2). Comparisons with norms of fertility established for agricultural soils of Alaska indicate alder soils to be very high in nitrate, low to medium in phosphate, and medium in potash contents (Table 3).

TABLE 2. Comparisons of A_1 horizon of soils under Sitka alder and neighboring herbaceous communities, Little Susitna Valley north of Palmer, Alaska

Community type	No. of soil pits	Carbon	Nitrogen	pH
		------ *Percent* -------		
Alder	24	27.0	1.42	3.6
Herbaceous	22	15.5	.83	4.5

TABLE 3. Comparisons of indicated amounts of NO_3, P_2O_5, and K_2O in soils under alder with agricultural soils of Alaska

Nutrients	Average of A_1 and B horizons from two alder sites	Norms based on several thousand agricultural soil samples of Alaska —	
		Low fertility	High fertility
	-------------------- *Pounds per acre* ---------------		
NO_3	130.8	24	80
P_2O_5	15.5	8	40
K_2O	184.5	80	320

Discussion

SOME PRACTICAL ASPECTS

The soil nutrient values and the amount of growth produced annually in this Subalpine Zone imply an exploitable productive potential. Eight to 14 dm of herbaceous growth accrue in taller communities, mostly within a 6- to 7-week period beginning in June. Some of the most extensive grasslands readily accessible for grazing occur in this zone on the Kenai Peninsula and Kodiak Island where the principal efforts of beef raising are concentrated.

The alder thickets are considered a nuisance, however, and often are burned to eliminate them. Two or more burnings are generally required. The highly organic and extremely acidic nature of the soil generated under alder poses a serious problem for the establishment of crops. Plants cultivated on alder sites in the Subalpine Zone do very poorly without sufficient and proper fertilization of the soil. Investigations have yet to be conducted on the use of alder as a biological source of nitrogen in a managed agricultural program. Much research is needed to learn how best to manage this subarctic soil.

Alder is sought for one direct use. Many natives and other Alaskans consider it a prime fuel for smoking salmon. Furthermore, it provides cover for moose (*Alces alces* var. *gigas* Miller) and bear (*Ursus americanus* Pallas, *U. arctos* L.) that inhabit the zone. Moose reject the unpalatable alder as browse, however, while feeding on willows intensely. Bear feed on grass and other herbaceous shoots that occur in the zone. The deep snow accumulations, which supply salmon-spawning and trout-bearing streams, generally remain longer under alder in this zone.

ZONAL RELATIONSHIPS

Aside from Hultén's reference to a subalpine vegetation type containing alder on the easternmost Aleutian island, there appears to have been no formal attempt at fitting the alder/tall herb association into a vegetational system of classification for south-central Alaska. Analytical work on this vegetation type has been performed by Hanson (1951) and Rieger and Wunderlich (1960) without reference to zonal relationships. Sigafoos (1958) mapped and discussed forested and treeless regions of Alaska but did not designate a subalpine vegetation type. He referred to a shrub tundra type, including thickets of willows, alder, and dwarf birch, occurring mainly along streams and lake banks within herbaceous tundra regions, but eliminated alder, willows, and aspen from consideration as dominant species "owing to their apparently temporary existence in forest development." Colinvaux (1967) noted that it was the custom of alder to advance ahead of the treeline in southwestern Alaska.

The question of whether the alder/tall herb association is but a seral stage in postglacial forest development requires a consideration of the time permitted for revegetation by trees and the effects of fire. Heusser (1965) cites evidence of a relatively late postglacial arrival for forests on the lower Kenai Peninsula. Griggs (1934) has proposed, with good evidence, that the forest on Kodiak Island is advancing, trees having occupied the island only recently. He suggested further that the treeline was advancing elsewhere in Alaska. But recent findings of Colinvaux (1967) indicate that the position of the spruce forest in the Late-Wisconsin glacial period in unglaciated southwestern Alaska may have been well advanced over its current position. Moreover, Hansen's work (1953), more pertinent to the area of this study, indicates a relatively early arrival for birch and spruce on glaciated terrain in the upper Cook Inlet region. Pollen of the two trees occurred in abundance toward the bottom of peat cores sampled to gravel in the vicinity of Anchorage.

The Matanuska Glacier receded from this vicinity and the lower valley well over 8,000 years ago (Williams and Ferrians, 1961). Ample time appears to have elapsed for trees to have vegetated glacial till since their arrival in the upper Cook Inlet region.

Zonal relationships are complicated by the effects of fire. Fire obviously has permitted establishment of the subalpine type of association on slopes below timberline in the upper Cook Inlet region. But downed logs and regeneration of Alaskan paper birches (*Betula resinifera* Britton, *B. kenaica* Evans), spruce, and poplar, particularly that of birch, divulge the former presence of forests on these slopes. Paper birch is absent from the Subalpine Zone, though small scattered stands and individual trees of spruce and balsam poplar may be present. But no real evidence of the prior existence of a forest has been found where the subalpine association is well developed.

Despite the apparent difference in duration of forest development for the coastal and upper Cook Inlet regions, forested and Subalpine Zones are delimited on glacial till within a brief altitudinal span in both regions. The development and persistence of this Subalpine Zone apparently is a response to a complex of environmental conditions. Altitudinal variations in timberline and the associated occurrence of the Subalpine Zone attest to this response. The lower timberlines and more extensive Subalpine Zones occur in the moist and cool situations. The drier slopes do not support a Subalpine Zone. Further, the alder representation in pollen profiles (Heusser, 1965) has fluctuated in the past apparently in response to postglacial climatic changes. Under proper conditions, the subalpine association appears capable of maintaining itself as a prevailing climax against both the forest below and various alpine communities above.

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A comparison of rhizosphere microfloras associated with mycorrhizae of red alder and Douglas-fir[1]

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Abstract

Rhizosphere microfloras of Cenococcum graniforme *(Sow.) Ferd. and Winge mycorrhiza of Douglas-fir (*Pseudotsuga menziesii *(Mirb.) Franco), of one type of ectotrophic mycorrhiza of red alder (*Alnus rubra *Bong.), and of nonmycorrhizal suberized roots of both tree species were investigated. Microbial populations and the most probable numbers of ammonifying and nitrate-reducing microbes differed qualitatively and quantitatively between rhizosphere microhabitats. In manometric studies, homogenized Douglas-fir nonmycorrhizal suberized root and red alder mycorrhizal root suspensions highly stimulated respiration of nonrhizosphere microbes, especially in the presence of glucose. Glucose oxidation, however, was suppressed in the presence of Douglas-fir mycorrhizal root suspension, probably by the antibiotic which the fungal symbiont,* C. graniforme, *is reported to produce. Glucose oxidation by nonrhizosphere microbes was similarly repressed in the presence of red alder nonmycorrhizal root suspension. An antagonistic substance found in red alder root and nodule suspensions inhibited growth of* Bacillus subtilis *(Cohn) Prazmowski and* B. cereus *Frankland and Frankland on glucose-salts agar. These experimental results are discussed with reference to the influence of mycorrhizal and adjacent nonmycorrhizal suberized roots upon rhizosphere microfloras.*

Introduction

The term "rhizosphere" was first introduced by Hiltner in 1904 to designate the region of soil immediately influenced by plant roots. Numerous investigators have since reported higher microbial activity and populations in the rhizosphere of many plants than in adjacent soil (Katznelson et al., 1948; Clark, 1949; Starkey, 1958; Rovira, 1965; and Timonin, 1965). However, little has been published on the influence of mycorrhizae on

rhizosphere microfloras. Tribunskaya (1955) compared the rhizosphere microfloras of 5-month-old pine seedlings lacking or having poorly developed mycorrhizae with those of similarly aged seedlings with well-developed mycorrhizae. She found considerably higher populations of fungi and proteolytic and fluorescent bacteria in rhizosphere soil of mycorrhizae than that of nonmycorrhizal roots. Katznelson et al. (1962) observed higher bacterial and actinomycete populations but lower numbers of fungi in the rhizosphere of yellow birch mycorrhizae than in that of nonmycorrhizal roots. The influence of mycorrhizal fungi upon the rhizosphere of a single Douglas-fir tree was demonstrated by Neal et al. (1964) who compared (1) three morphologically distinct mycorrhizae, sometimes side by side on the same rootlet, (2) adjacent suberized roots, and (3) nonrhizosphere soil. Each mycorrhizal rhizosphere differed significantly from the others in populations of bacteria, fungi, and *Streptomyces*, the difference being attributed to the type of fungal symbiont present. The suberized roots and nonrhizosphere soil differed from the mycorrhizae as well as from each other.

The present study was initiated as part of a broad investigation of soil microbes in relation to biological control of tree root disease. Red alder was included in the study because preliminary investigation suggested its possible role in inhibiting certain root pathogens (Li et al., 1968) and because of its ecological significance in forests of the Pacific Northwest as a nonleguminous, nitrogen-fixing tree (Tarrant, 1961; Chen, 1965).

Materials and Methods

Ectotrophic mycorrhizae, suberized roots, and adjacent nonrhizosphere soil were collected from the upper 8 inches of soil in a pure stand of red alder and, for Douglas-fir, from a mixed-conifer stand lacking alder at the Cascade Head Experimental Forest near the northern Oregon coast. Samples were stored at 1 C and processed within 24 hours after collection.

Examination of root collections revealed that each tree species had an abundance of distinctive, identifiable, ectotrophic mycorrhizae. For Douglas-fir, the distinctive mycorrhizal type was formed with *Cenococcum graniforme* (Sow.) Ferd. and Winge, a fungus that commonly forms mycorrhizae on Douglas-fir throughout the region (Trappe, 1962). For alder, the distinctive mycorrhiza was dark brown and rough, formed by an unidentified basidiomycete (Neal et al., 1968). These two types were used in our experiments. Nonmycorrhizal suberized roots were taken from the same collections in lieu of nonmycorrhizal root tips, which could not be found. Three 1-kg portions of nonrhizosphere soil were collected from near the sampled roots at each sampling location.

Samples were taken from three locations in each stand, each sample being analyzed independently as a replicate.

Rhizosphere and nonrhizosphere microbial populations were estimated by the dilution pour-plate method on soil extract agar (Allen, 1957) for bacteria, and on Martin's (1950) rose bengal agar for molds, as described by Neal et al.

(1964), Neal et al. (1966), and Neal et al. (1968). The most probable number of microbes capable of producing ammonia from peptone water and those reducing nitrate to nitrite in 1-percent KNO_3 broth were determined according to the method of Alexander (1965). After 7 days' incubation at 28 C, ammonia production from peptone water was detected by Nessler's reagent, and the presence of nitrites, indicating the reduction of nitrate in 1-percent KNO_3 broth, was determined by Griess' reagent (Pelczar, 1957).

In metabolic studies, respiration was measured by the direct method (Umbreit et al., 1957). Mycorrhizal and adjacent suberized roots from Douglas-fir and red alder, respectively, were severed from the main roots, cleaned ultrasonically, surface sterilized in 2-percent sodium hypochlorite solution for 5 min, and serially washed in sterile distilled water. The roots were homogenized by a Carver hydraulic press at 10,000 psi. The root slurry was collected aseptically and adjusted with sterile 0.1-M (molar) phosphate buffer, pH 6.5, to a final volume containing 20.0 mg of root material, ovendry basis, per ml of root suspension. Ten grams, ovendry basis, of non-rhizosphere soil sieved through a 40-mesh screen were added to 100 ml of sterile 0.1-M phosphate buffer, pH 7.0. One ml of the resulting soil-buffer suspension, vigorously shaken, was added as inoculum to each Warburg flask, which also contained 0.5 ml of root suspension (10 mg of root material, ovendry basis), 0.5 ml of 0.1-M phosphate buffer, pH 7.0, 0.2 ml of 20-percent KOH in the center well fitted with fluted filter paper to absorb carbon dioxide, and 0.5 ml of 0.1-M glucose in the flask sidearm. Controls of KOH with soil inoculum only, root material only, and root material plus glucose were included. A sufficient volume of 0.1-M phosphate buffer, pH 7.0, was added to each flask when needed to bring the total liquid volume to 3.0 ml. Duplicate flasks of each treatment were attached to calibrated manometers and placed in a constant-temperature water bath held at 29.5 C. The flasks were allowed to equilibrate 1 hr before the manometers were closed. Glucose solutions previously pipetted in the flask sidearm was tipped in immediately after equilibration.

Assays for biologically antagonistic substances in red alder roots and nodules were determined by the paper-disk plate method (Loo et al., 1945) with stock cultures of *Bacillus cereus* Frankland and Frankland and *B. subtilis* (Cohn) Prazmowski. Root and nodule slurries were prepared as previously described from material collected during the summer and winter months and concentrated approximately fiftyfold by lyophilization. Paper disks were impregnated with the slurry suspensions, placed on peptone-beef extract and glucose-salts agar seeded with the test organisms, and incubated for 48 hr at 30 C. Controls were paper disks impregnated with sterile distilled water.

Results

BACTERIAL POPULATIONS

Rhizosphere microbial populations of mycorrhizae formed by *C. grani-forme* and of adjacent suberized roots of Douglas-fir were greater than those

of nonrhizosphere soil (Table 1). The R/S ratios (rhizosphere microbial population/nonrhizosphere soil microbial population) were 3.3/1 and 4.3/1, respectively, agreeing with results of other studies on a variety of plants (Rovira, 1965).

Bacterial populations in red alder mycorrhizal and suberized root rhizospheres were substantially higher than nonrhizosphere soil; the R/S ratios were 16.6 and 8.6, respectively.

TABLE 1. Microbial population estimates of rhizosphere and nonrhizosphere soil

Rhizosphere soil type	Bacteria	R/S ratio[1]	Molds	R/S ratio[1]
	Millions[2]		*Thousands*[2]	
Douglas-fir mycorrhizal root	91.6	3.3	347.3	2.0
Douglas-fir suberized root	120.0	4.3	300.0	1.7
Red alder mycorrhizal root	580.2	16.6	455.9	2.3
Red alder suberized root	300.7	8.6	275.0	1.4
Douglas-fir nonrhizosphere soil	28.0	–	175.0	–
Red alder nonrhizosphere soil	35.0	–	200.0	–

[1] *Rhizosphere/nonrhizosphere soil ratio.*
[2] *Counts per gram of soil, ovendry basis. Each value represents a mean of three replicate samples.*

MOLD POPULATIONS

Mold populations were higher in the rhizosphere of mycorrhizal and suberized roots of Douglas-fir and red alder (Table 1) as compared with nonrhizosphere soil. Differences between mycorrhizal and suberized-root microhabitats of Douglas-fir were slight (R/S 2.0 and 1.7, respectively). For red alder, however, mold populations were more than 1-1/2 times as great in the mycorrhizal rhizosphere as in the suberized root rhizosphere (R/S 2.3 and 1.4, respectively). The rhizosphere mold population increases agree generally with those reported by Tribunskaya (1955) but not with those found by Katznelson et al. (1962) and Neal et al. (1964).

PHYSIOLOGICAL GROUPS

Members of the different physiological groups were much more numerous in the rhizospheres of mycorrhizae and suberized roots of Douglas-fir and

red alder than in nonrhizosphere soils (Table 2). The most probable number of ammonifying and nitrate-reducing microbes in the rhizosphere of Douglas-fir mycorrhizae differed little from that of nonmycorrhizal suberized roots. However, in rhizospheres of red alder mycorrhizae, more than three times the number of ammonifying than nitrate-reducing microorganisms were observed. The opposite was found in the rhizosphere soil of suberized roots; the nitrate reducers were approximately three times greater than the number of ammonifying microorganisms.

METABOLIC ACTIVITY

The influence of Douglas-fir and red alder root suspensions on metabolic activity of nonrhizosphere microbes is shown in Figures 1 through 4. Results are expressed as microliters of oxygen uptake beyond that of endogenous respiration (soil only). A successful attempt was made in the studies to simulate an artificial rhizosphere in a Warburg flask by modifications of the sterile sand and collodion membrane techniques (Rovira, 1956; Timonin, 1941).

The metabolic activity of the nonrhizosphere soil microflora was stimulated by a slurry of Douglas-fir nonmycorrhizal roots (Fig. 1). After 12 hours, oxygen uptake was 1-1/2 times as great as nonrhizosphere soil plus glucose. Combining the root slurry with glucose caused a substantial increase in microbial activity as shown by increased oxygen uptake, the increase being approximately 2-1/2 times greater than the oxidation rate of nonrhizosphere soil plus glucose.

TABLE 2. Most probable numbers of ammonifying and nitrate-reducing microorganisms

Rhizosphere soil type	Ammonifiers[1]	Nitrate reducers[2]
	------ Millions[3] ------	
Douglas-fir mycorrhizal root	74.3	46.1
Douglas-fir suberized root	64.3	50.1
Red alder mycorrhizal root	128.8	47.3
Red alder suberized root	39.1	120.4
Douglas-fir nonrhizosphere soil	18.3	8.6
Red alder nonrhizosphere soil	17.5	25.3

[1] *Producing NH_4^+ in peptone water.*
[2] *Reducing NO_3^- in nitrate broth.*
[3] *Numbers per gram of soil, ovendry basis. Each value is the mean of the most probable number values for three replicates.*
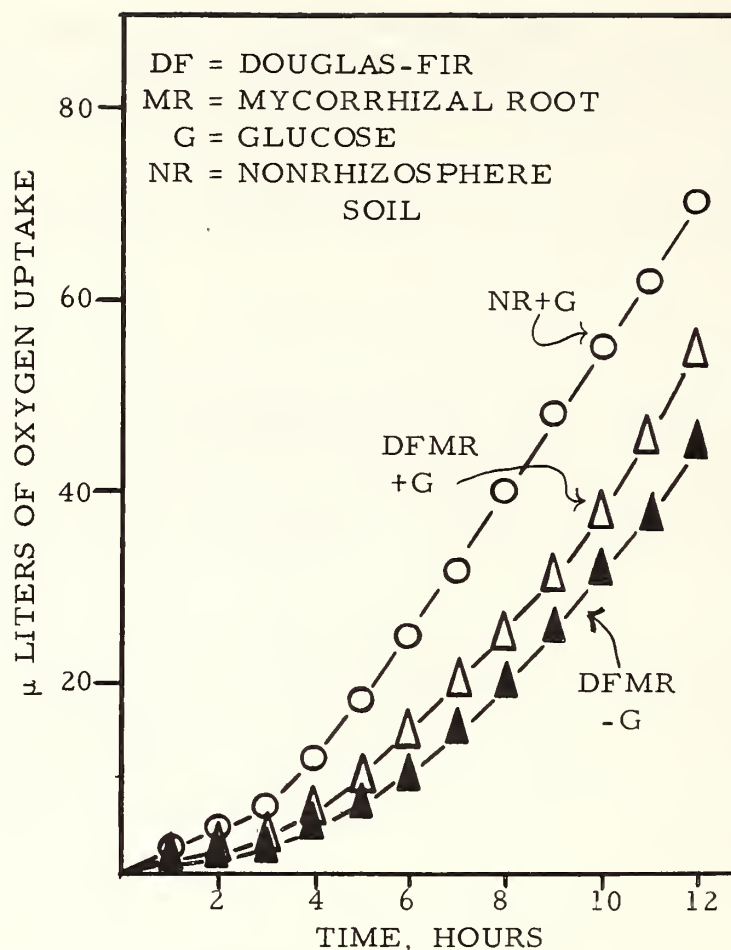
Figure 1. Microbial oxidation of Douglas-fir nonmycorrhizal suberized root slurry with and without glucose (microliters of oxygen uptake beyond endogenous respiration of soil only.

The opposite effect was produced by a slurry of Douglas-fir mycorrhizae formed by *C. graniforme,* an antibiotic-producing fungus (Krywolap and Casida, 1964; Krywolap et al., 1964) (Fig. 2). The oxidation rate was appreciably less than nonrhizosphere soil plus glucose. Adding glucose with the mycorrhizal root slurry caused little increase in oxygen uptake; oxygen consumed was still less than for nonrhizosphere soil plus glucose.

Metabolic activity was greatly stimulated by adding red alder mycorrhizal suspension to nonrhizosphere soil with glucose (Fig. 3). Oxygen uptake increased to 3-1/2 times that of soil and glucose alone.

The influence of red alder nonmycorrhizal suberized root slurry on the oxidative respiration patterns of nonrhizosphere soil microbes is shown in Figure 4. The microbial oxidation rate was considerably less in the presence of red alder suberized root slurry in comparison to nonrhizosphere soil plus

glucose. Adding glucose with the suberized root slurry caused little additional stimulation of microbial metabolic activity.

These oxidative respiratory patterns are similar to those obtained for Douglas-fir mycorrhizal rootlets formed by *C. graniforme,* suggesting an inhibitory phenomenon here as well. To explore this possibility, an anti-bacterial substance in red alder root and nodule slurries was sought by the paper-disk technique. Slurries prepared from summer collections effectively inhibited *B. cereus* and *B. subtilis* on glucose-salts agar but not on peptone-beef extract agar. Slurries prepared from winter collections after leaf fall were not inhibitory on either medium.

Discussion and Conclusions

The data suggest that the microfloras surrounding mycorrhizae of Douglas-fir and red alder are influenced quantitatively by the fungal symbiont present.
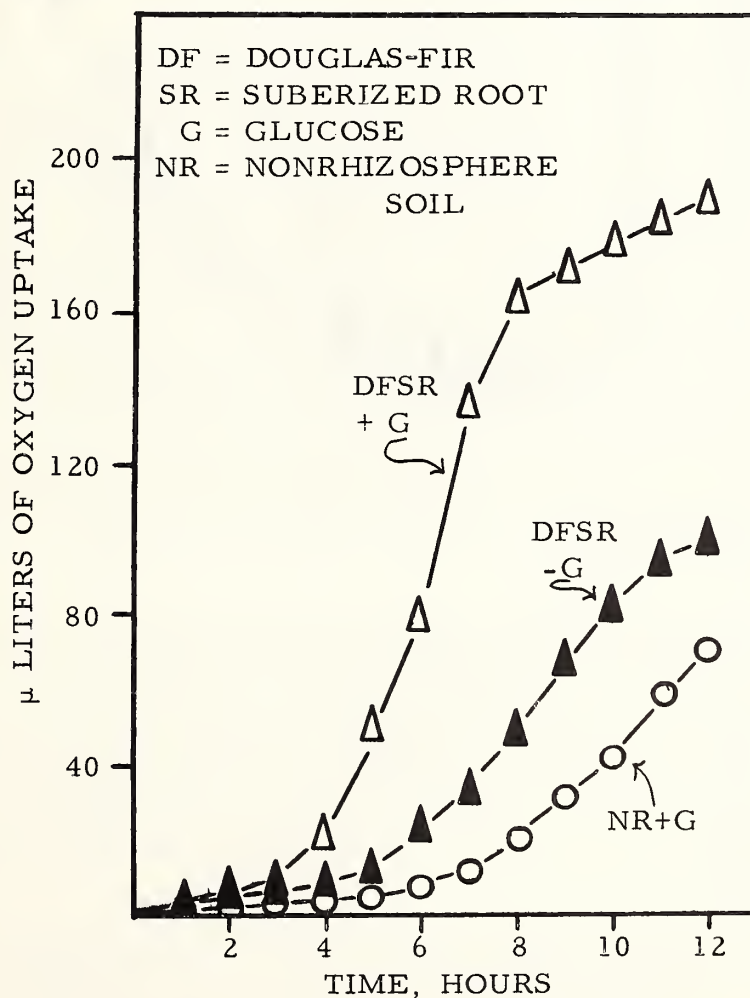
Figure 2. **Microbial oxidation of Douglas-fir mycorrhizal root** (*Cenococcum graniforme*) **slurry with and without glucose (as in Fig. 1).**
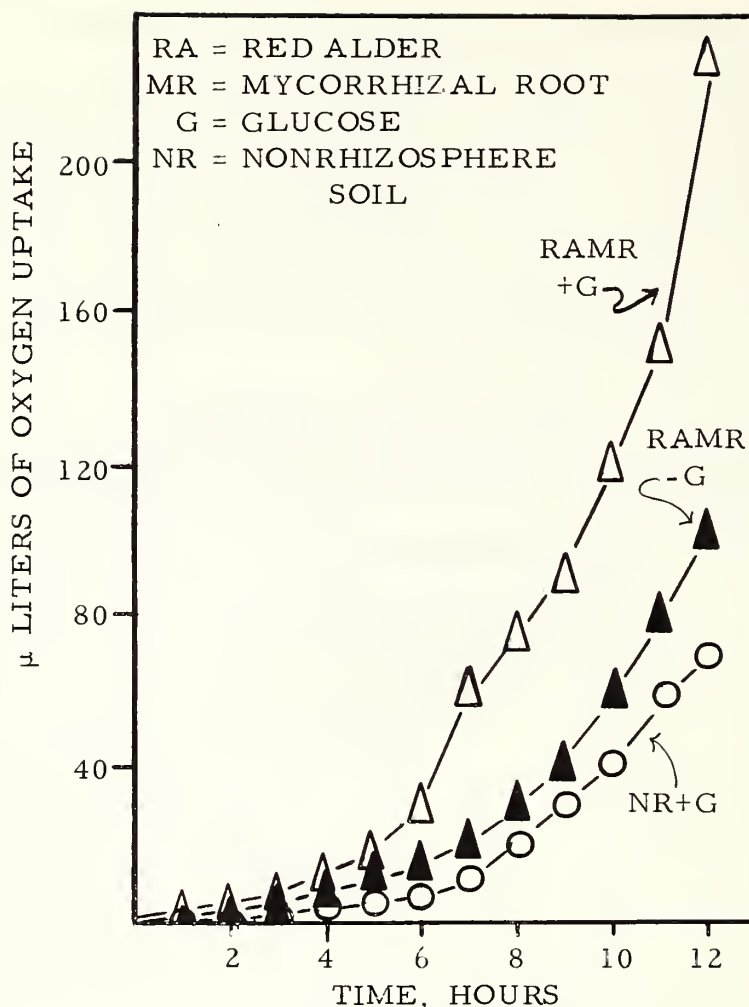
Figure 3. **Microbial oxidation of red alder mycorrhizal root slurry with and without glucose (as in Fig. 1).**

The distinct differences in microbial populations found in each rhizosphere as compared with nonrhizosphere soil (Table 1) can be attributed to the influence of the mycorrhizal fungus. Population differences may be due to the excretion of inhibitory or stimulatory substances by the fungal symbiont, host plant, or both into the rhizosphere thus favoring a selective development of microorganisms in each microhabitat. Selective absorption of organic or inorganic nutrients by the mycorrhizal fungi also may influence the rhizosphere.

The data in Table 2 show the existence of different selected physiological groups which are stimulated in each microhabitat as compared with nonrhizosphere soil. These observations are similar to those of Katznelson et al. (1962) and Neal et al. (1964). Numerical differences as related to physiological activity are not great between Douglas-fir mycorrhizal and nonmycor-

rhizal rhizospheres but do differ appreciably between these rhizospheres for alder.

The greater numbers of various microbial physiological types suggest a direct influence on availability of nutrients to the tree, particularly with respect to nitrogen. For example, a more rapid breakdown of amino acids to elemental nitrogen in rhizosphere than in nonrhizosphere soil has been reported by Katznelson and Rouatt (1957). Changes in acidity near bean roots have been observed to alter ammonium assimilation (Barker et al., 1966).

The apparent influence of mycorrhizae on associated microorganisms could possibly affect the susceptibility of roots to invasion by pathogenic fungi either by selective stimulation or inhibition of microbial groups. As suggested by Zak (1964) and Neal et al. (1964), the metabolic products of these microbial groups found in the rhizosphere also may alter the environment of the root microhabitat by changing its acidity, producing antago-
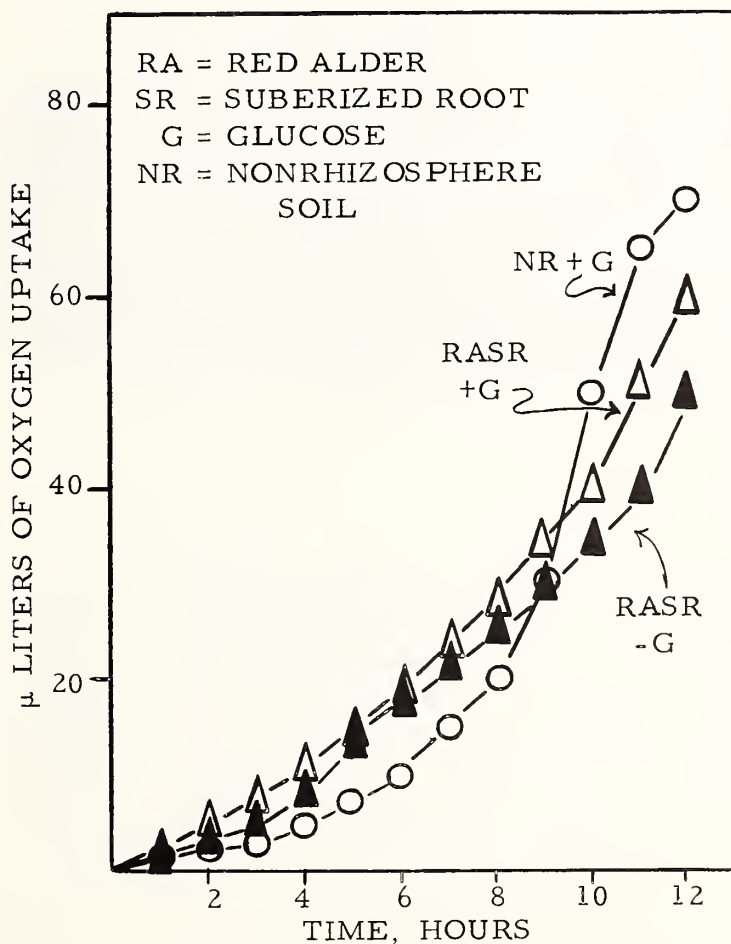
Figure 4. Microbial oxidation of red alder nonmycorrhizal suberized root slurry with and without glucose (as in Fig. 1).

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nistic materials, or selectively assimilating nutrients, thus forming an effective biological barrier to root pathogens.

Root exudates and decaying root material or sloughed-off cells are generally thought to exert the greatest influence on microorganisms in the rhizosphere (Rovira, 1965). Healthy plants, and probably diseased plants, exude a wide variety of organic compounds (Rovira, 1965). However, the amounts of exudate and cellular debris available to rhizosphere microorganisms at any one time are not known.

In our experiments, the amount of stimulation depended upon the root material associated with each microhabitat investigated. Exudates from different plants as well as different strains of the same plant species exert markedly different effects upon the rhizosphere microflora (Rovira, 1965).

In particular, activity of the nonrhizosphere microflora differed in relation to metabolism of glucose. Metabolic activity was appreciably stimulated by addition of glucose to the Warburg flask containing Douglas-fir suberized root material (Fig. 1), but when glucose was incorporated with Douglas-fir mycorrhizal material, little oxidative respiration increase was observed. If more than one substrate is available as a carbon source, all other factors being equal, microorganisms will utilize the carbon source which requires the least amount of energy to degrade and assimilate.

Glucose is easily utilized with a minimum of energy expenditure by most microorganisms and in most cases is utilized preferentially by microbial cells. Thus, one could expect the oxidation rates with mycorrhizae plus glucose to be nearly the same as those obtained with soil only plus glucose or to be considerably higher as with Douglas-fir suberized roots (Fig. 1). This not being the case, however, a selective inhibition of microbial oxidation was indicated, presumably due to the antibiotic produced by the fungal symbiont, *C. graniforme* (Krywolap and Casida, 1964; Krywolap et al., 1964). Although the results are not conclusive, it appears that the antibiotic effectively inhibited the utilization of glucose as an energy source by certain groups of bacteria. Even though the antibiotic was not water soluble, the results indicate it had an active influence in the rhizosphere (Fig. 2, Tables 1, 2). The mycorrhizal fungus directly influences the rhizosphere microflora by its metabolic products and thus selectively stimulates or inhibits specific microbial groups.

The red alder mycorrhizal root slurry stimulated considerably the metabolic activity of nonrhizosphere microbes (Fig. 3). Incorporating glucose brought about an even greater response. The results indicate the mycorrhizal root material to be highly stimulating and agree with data presented in Tables 1 and 2.

A metabolic oxidation rate pattern similar to that obtained with mycorrhizal roots of Douglas-fir formed by *C. graniforme* also was observed with red alder root material (Fig. 4). However, incorporation of glucose with the root slurry did not cause an appreciable increase in metabolic activity, indicating the presence of an inhibitory substance, particularly with reference to glucose oxidation. Polyhydroxy phenols, reported to retard glucose oxida-

tion of selected pure cultures of bacteria (Basaraba, 1966), could possibly have been responsible for the inhibition.

A biological assay for antagonistic materials in red alder spring and summer roots and nodules (Fig. 5) revealed a substance which effectively inhibited the growth of *B. cereus* and *B. subtilis* on glucose-salts media but not on peptone-beef extract agar. Extracts of root and nodule materials collected during winter months did not contain substances inhibitory toward the bacilli.

The identity or action of this substance or substances from red alder is not known, but its nature probably lies in one or more of three areas. First, oxidized polyphenols have been implicated as defense mechanisms against root-attacking microbes (Hare, 1966). The methods of preparing the root and nodule extracts may have triggered the oxidation of phenolic materials by polyphenol oxidases to biologically toxic quinones. These phytotoxic compounds may have been responsible for the growth inhibition of the
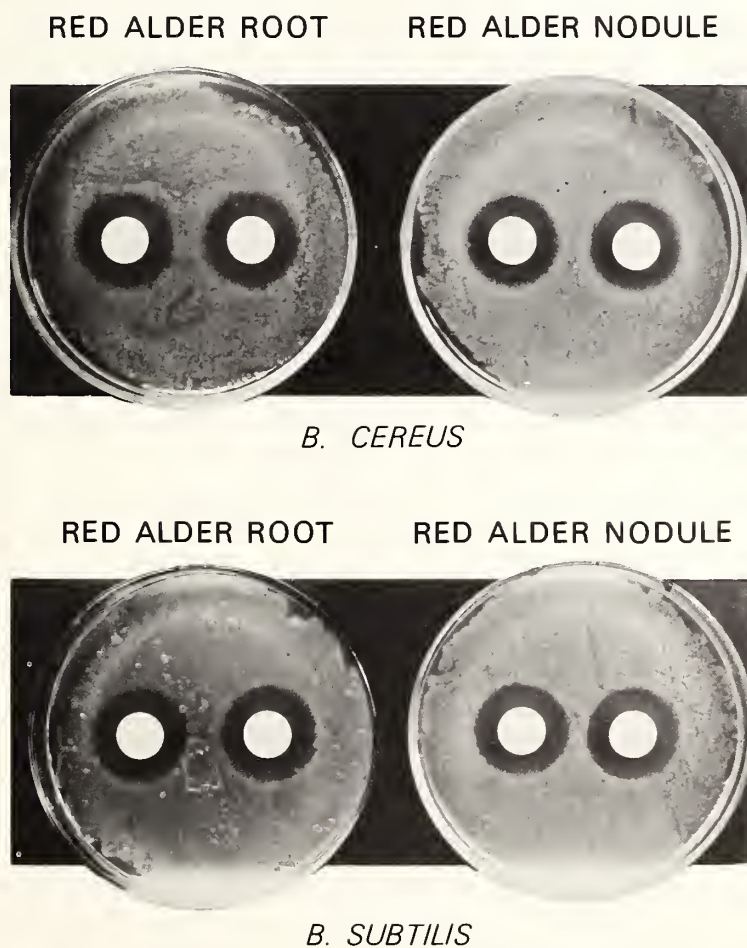
Figure 5. Growth inhibition of *Bacillus cereus* and *B. subtilis* by red alder root and nodule extracts on glucose-salts medium (as in Fig. 1).

bacilli observed on glucose-salts medium. Li et al. (1968) have demonstrated polyphenol oxidase activity in leaf extracts of red alder; no activity was observed with Douglas-fir needle extracts. Inhibition of glucose oxidation by the red alder suberized root material (Fig. 4) and uninhibited growth of the bacilli on peptone-beef extract agar supports this possibility. These phytotoxic compounds may not ordinarily be active in the rhizosphere, however, since polyphenol oxidase is usually not activated until root tissues are injured (Hare, 1966). Our data show that the red alder suberized root microhabitat fosters a highly active rhizosphere microflora (Tables 1 and 2).

Secondly, an antibiotic produced by the red alder nodule endophyte may have been present in the root and nodule extracts and effectively inhibited the growth of bacilli (Fig. 5). Based upon studies of other species of *Alnus* (Uemura, 1952a; Uemura, 1952b; and Mikola, 1965), the nitrogen-fixing endophyte of red alder nodules was presumably a *Streptomyces* species. Mikola (1965) found that several *Streptomyces* species isolated from *Alnus glutinosa* (L.) Gaertn. nodules produced antibiotics which effectively inhibited growth of *Fomes annosus* (Fr.) Cooke, a root pathogen. The strongest antagonism was exerted by strains capable of forming nodules with the host plant in controlled inoculation experiments. Considine and Casida (1964) observed that certain species of *Streptomyces* could grow and produce antibiotics on nitrogen-deficient media.

Cytological observations have shown the *A. glutinosa* endophyte changes morphologically from an active stage in the summer to a resting stage after leaf fall during the winter months (Gardner, 1965). This could explain the lack of inhibitory substances in root and nodule extracts obtained from material collected during the winter months. The influence of an antibiotic upon the rhizosphere microflora may be negligible since its action would depend upon its concentration in the rhizosphere. Bacteria are well known for their ability to mutate to antibiotic-resistant strains, especially if the antibiotic is present in sublethal concentrations.

If both the production of an antibiotic and oxidation of phenolic compounds to quinone should be active at the same time, a synergistic action may result. Vörös et al. (1957) have reported that *in vitro* streptomycin is ineffective against *Phytophthora,* but when absorbed through the roots, the antibiotic confers resistance and enhances polyphenol oxidase activity. If this is the case, lack of either antibiotic production or polyphenol oxidase synthesis may be the reason no inhibitory substances were found in extracts of root and nodule material during the winter months.

These results indicate the rhizosphere microbes of Douglas-fir and red alder are influenced qualitatively and quantitatively by the mycorrhizal fungus present. Metabolic secretions of the mycorrhizal fungus and associated suberized roots probably play an important role in influencing the kind and type of microorganisms that are to be found in each microhabitat. The importance of these excreted metabolites is not fully known, but they could be important in discouraging attack of roots by parasites by favoring the development of specific rhizosphere microbes which form a biological barrier.

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Role of red alder in western Oregon forest succession

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Abstract

Red alder was studied to determine influence on long-term forest succession. Juvenile growth of alder appears responsible for failure of other species, particularly conifers, to maintain positions of dominance. Success of Douglas-fir depends on delay of 4-9 years in establishment of alder, or occurrence of the two species at such a spacing that Douglas-fir will be from 8 to 10 years old before encroachment by alder.

Alder is concentrated on mesic sites with history of scarification or fire. Dense stands were shown to fix nitrogen at an annual rate of about 320 kg per hectare on nitrogen-deficient soils. Equilibration of fixation with nitrogen in soil tends to occur before the age of 20 years, beyond which contributions of nitrogen are small.

Common successors to alder include salmonberry, vine maple, and hazel, in that order. Western hemlock may follow eventually, but Douglas-fir is virtually absent except where it develops concurrently with the alder in openings within the alder stand.

Red alder (*Alnus rubra* Bong.) is well known for its capacity to fix atmospheric nitrogen and to dominate sites on which growth of conifers is desired. Alder has been described variously as a pioneer species with a major role in soil development, a source of protection for emerging conifers, a commercial forest type, and a brush species of no appreciable beneficial impact. The alders have received intensive study with regard to some basic ecological functions and their role in soil development. Most of the reports of long-term influence in development of climax forest types have been limited to local special circumstances, or have been based on speculative descriptions of vegetation development in existing older stands. We offer the hypothesis that the occurrence of red alder after some disturbance has a profound effect on forest development, and that nitrogen fixation plays an important but secondary role in determination of later stages in succession. Mathematical models have been developed that help predict capacity of Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) to replace alder.

Review of Literature

A great wealth of literature pertains to behavior of various alders, of which perhaps black alder (*A. glutinosa* (L.) Gaertn.) has received the most

attention. Because of similarity between the reported habits of black and red alders, some findings pertaining to black alder have been used as background for this study.

Juvenile habits of pioneer species determine ultimately the amount of space each will occupy in the dominant community. Red alder is known as a pioneer of vigorous juvenile growth, able to outstrip coniferous associates for the first 25 years (Fowells, 1965). More specifically, growth from 6 to 18 inches during the first year is common on good sites; the trees may reach some 18 ft. by the fifth year, and up to 40 ft. in height by the age of 10 years. Worthington et al. (1960) derived yield equations that predicted heights of about 48 and 37 ft. at 10 years on best and average sites for western Oregon and Washington. Even on the poorest sites for alder, growth of about 24 ft. at 10 years is predicted. Height-growth curves for alder are negatively curvilinear from a very early age. Height increment is greatest from 3 to 5 years after establishment, after which there is a gradual decrease in annual increment until maximum height is reached.

Growth rates of conifers during the first 20 years in the field have received only cursory attention. Early growth of Douglas-fir has been studied by Ching (1964) as a means of comparing growth rates of seedlings of various origins on comparable sites. His data are restricted to the first 5 years of growth but give a good estimate of inherent growth characteristics for this period based on adequate sample size and many types of planting stock. Warrack and Fraser (1955) expressed growth of Douglas-fir for 4- and 6-year periods after reaching breast height as linear functions of site quality, but did not attempt to characterize pattern of growth before that time. McArdle and Meyer (1949) express juvenile growth in terms of the numbers of years to reach 4.5 ft. in height for each site class, but do not integrate their data into a curve of height before the age of 20 years. Preliminary integrated curves of juvenile growth of Douglas-fir were reported by Newton (1964) as a means of illustrating competitive influence of various brush species. These curves were refined further in a later study that integrated several factors of site and vegetation in a growth equation that expressed height increment in terms of site factors and size of seedling or tree (Newton, 1967). These models closely approximate growth described in segments in the former studies, and tie in with growth curves derived for yield tables. Because of the apparent precision with which this model fitted field observations, a similar approach was used as a basis for smoothing and projecting stand development for this study.

Nitrogen fixed by pure stands has been studied in other species of alder to a much greater extent than for red alder. Laboratory studies have been used to demonstrate conclusively that alder has the capacity for fixation (Bond, 1958; Virtanen, 1957). Quantities of fixed nitrogen have been determined under various laboratory conditions, but have remained largely speculative in the field. Perhaps the work of Crocker and Major (1955), which illustrates the long-term cumulative effect of nitrogen and carbon accretion on outwash gravel, provides the best insight as to rates of fixation that can be expected in nature for a shrub species of alder growing on an

infertile site. They found that soil nitrogen under the influence of *Alnus sinuata* (Reg) Rydb. increased until the age of 50 years, after which alder was largely replaced by conifer forest type. There is a suggestion in their data that maximum annual increment of nitrogen occurs before the age of 40 years, a trend that is also reflected in accumulation of organic litter residues. Although authors attached no special significance to this trend, there may be a parallel with the tendency found by Zavitkovski and Newton (1967) in *Ceanothus velutinus* (Dougl.) stands, where maturity was correlated with equilibration of litter accumulation, followed by senescence with increasing importance of conifers in the stand. The same pattern may be found for red alder in the work of Tarrant (1961) who found annual increment of 56.5 pounds per acre of nitrogen in partial stands of alder, while Worthington et al. (1962) predicted succession to Douglas-fir by the sixtieth year.

In summary, the consensus of ecologists working with alder succession supports the contention that there is an improvement in soil fertility attributable to presence of alder, and that conifers are the likely successors for red alder. Conifer development presumably is enhanced by nitrogen contributions by alder. An important inconsistency is apparent, however, when the growth habits of conifers are compared with those of alder. Juvenile growth of conifers is less than that of alder, which relegates conifers to an understory status for an extended period. Because of the intolerant nature of Douglas-fir, the most common potential successor to alder, it is unlikely that an extended period of suppression can be tolerated. Moreover, understory species reported by Worthington et al. (1962) reduce the chance of Douglas-fir becoming established after alder stands mature.

Methods

Growth patterns and community development.—A range of soil and climatic conditions was sampled to determine factors that influence the capacity of red alder to completely dominate sites within its optimum range. Stands sampled were growing on both sedimentary and basic igneous parent material in climatic zones of similar temperature regimes but widely differing moisture balances. Generally, the plots were scattered along a rough transect extending from the Oregon coast at Hebo to the headwaters of the Middle North Fork of the Willamette River in the Cascade Range (Fig. 1). Eleven stands were sampled in the coastal slopes and 11 in the Willamette Valley slopes of the Oregon Coast Ranges, and 17 stands were selected in the Cascade Range up to 2,500 feet. All stands were between 4 and 25 years of age and were growing on scarified sites from which mature stands of Douglas-fir had been harvested.

Complete stem analyses of two or more randomly selected dominant alders were made for each stand to establish patterns of annual increment under specific site conditions. On the same site, the two closest open-grown Douglas-fir trees of the same age as the alder were measured by annual increment. Two or more suppressed Douglas-fir in the vicinity of the dominant alders were examined to determine their response to alder dominance. Each stand was described according to site factors, which included:
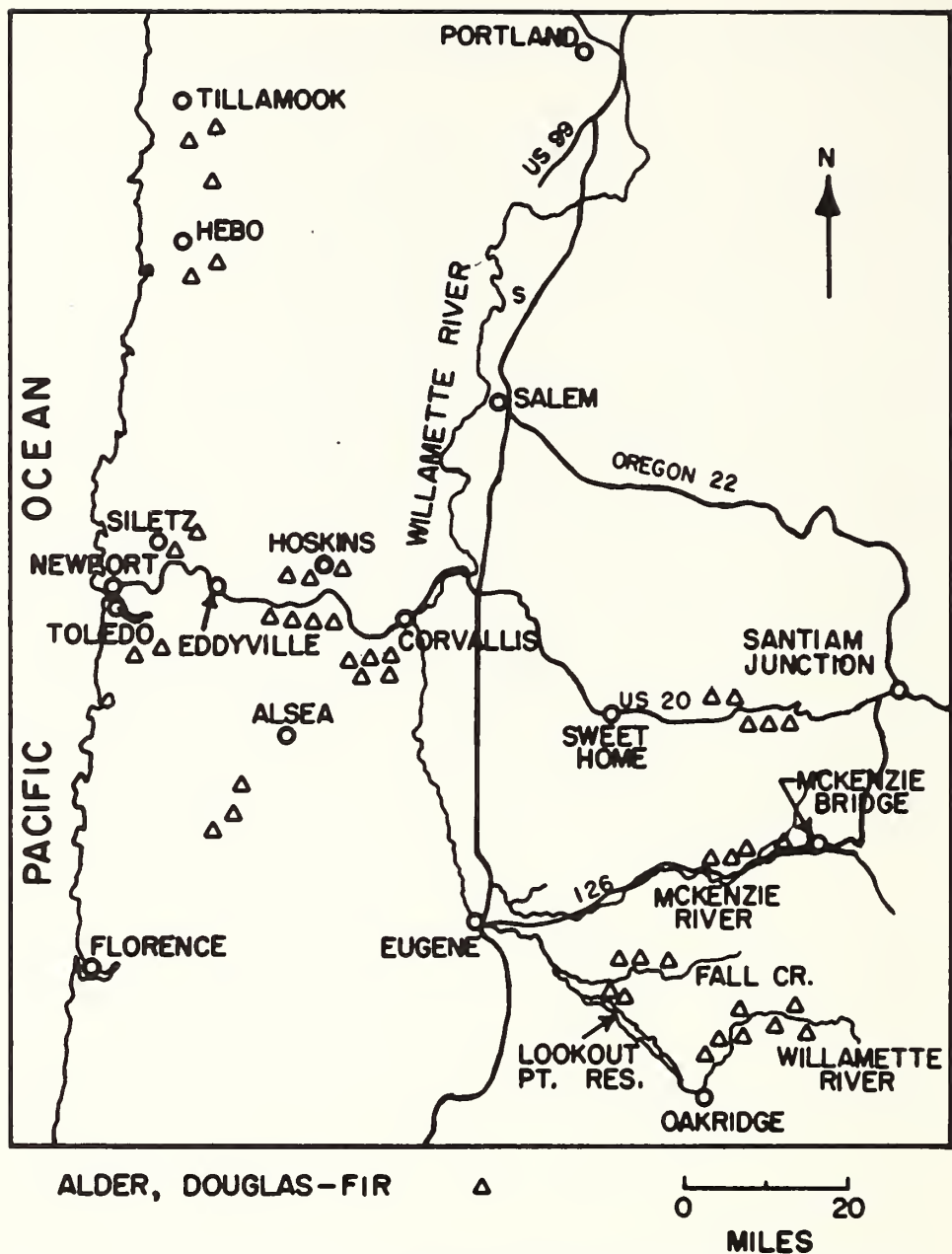
Figure 1. Map of central western Oregon with triangles that mark locations of sample plots.

moisture status, either well or poorly drained; percent of slope; azimuth of aspect; and elevation. Stands sampled included a good representation of moisture regimes, aspects, and slopes, but it was impossible to sample all conditions over the complete range of elevation. Moreover, there was undoubtedly some confounding between aspect and moisture status despite existence of riparian vegetation as indicators on all wet sites.

Mathematical models were derived for smoothing growth curves of both red alder and Douglas-fir in such a way as to permit extension of plot data

with curves in normal yield tables developed by Worthington et al. (1960) for alder and by McArdle and Meyer (1949) for Douglas-fir. The data processing program plotted actual and predicted growth, with annual growth expressed as the linear and quadratic functions of height at the beginning of each year of growth as follows:

$$\Delta H = \alpha + \beta_1 \ln H + \beta_2 (\ln H)^2 + \in,$$

when ΔH = annual height increment,

H = total height at beginning of growth year,

$\in$ = error, and

α, β_1, β_2 = regression constants.

Differences required in time of establishment so that Douglas-fir would be in a dominant position were calculated from the derived curves of growth of Douglas-fir and red alder. These values were determined from the difference in age of the two species when the growth in height of Douglas-fir exceeded that of alder (Fig. 2). Since the juvenile growth of Douglas-fir was never greater than that of alder, the reverse procedure was unnecessary. This difference in time of establishment needed to insure dominance of Douglas-fir will be referred to hereafter as the "adjustment period."

Compatibility of Douglas-fir and red alder growing on the same site was assumed to be related to length of the adjustment period, with a period of zero years indicating complete compatibility, but with compatibility decreasing as the adjustment period increases. Regression equations were derived on the basis of unweighted means to determine if the environmental variables had an important influence on the ability of Douglas-fir to succeed in the presence of alder. The equations were used to describe effects of moisture regime, degree of slope, and combined effects of moisture and slope. The adjustment period was the dependent variable in all calculations.

Nitrogen accretion.–Field estimates of nitrogen accretion were derived from calculations of total nitrogen in stands growing on subsoil and ranging from 0 to 62 years of age. Cutting records supplied by the U.S. Forest Service (Siuslaw National Forest) and several private parties provided histories of 36 stands growing on landings or other scarified sites where all surface soil had been removed during logging. Careful selection of sites was necessary to avoid confounding with logging residues, and only those stands were studied that were growing where there was clearly no appreciable residual organic matter at the time of establishment. These stands were selected with confidence up to the age of about 15 years; beyond this age, signs of contamination were increasingly obscured by contributions of the stand being studied. Flooding also may have influenced estimates on some sites. Sampling was restricted to those stands growing on soils derived from the Tyee sandstone formation to insure that soil nitrogen would develop from a common starting point.

Virtually all stands were pure red alder. Occasional individual shrubs of salmonberry (*Rubus spectabilis* (Pursh)) were found, but these did not
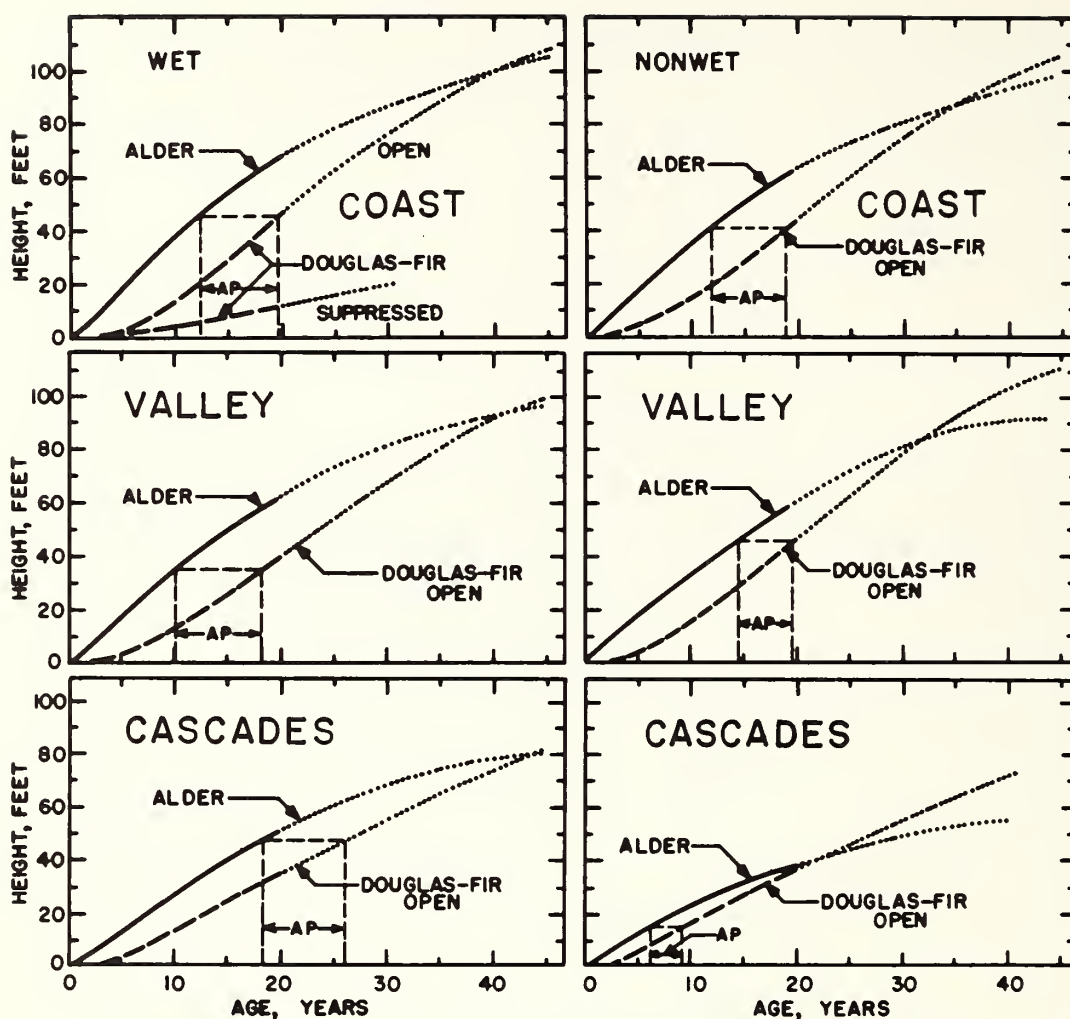
Figure 2. Growth of red alder and Douglas-fir on six comparable sites: top, western slope of the Coast Ranges; center, Willamette Valley slope of the Coast Ranges; bottom, western slope of the Cascade Range. Wet sites are on left, nonwet on right. Adjustment period for each site is indicated by length of line AP. Basic data produced solid and broken lines; dotted lines are from yield tables.

contribute appreciably to the over-all community composition in any stands less than 25 years of age.

Total soil nitrogen was calculated from samples that represented depths of 0-10 cm, 10-30 cm, and 30-60 cm, and that were adjusted for bulk density and stoniness. Six determinations were run for each stand, two at each soil depth. Nitrogen in biomass, obtained by analyses of representative samples of litter and above-ground parts, was added to soil nitrogen. All samples were analyzed by the Kjeldahl method.

Findings

Growth patterns and community development.—Red alder apparently cannot survive very long drying periods during germination, hence it is

restricted to scarified sites in much of its range. Once established, its growth is very rapid but slows after the third or fourth year. Associated species include a wide variety of forbs and shrubs with Douglas-fir almost always present. Most associated shrubs have a limited height potential and never develop rapidly or completely as long as alder is dominant. Douglas-fir and other conifers reach maximum rate of growth some 10 years later than alder, but the adjustment period is usually less because of the declining rate of alder growth while growth of conifers is increasing. The actual range of adjustments needed for the various site conditions and the general forms of the comparable growth curves of alder and Douglas-fir are shown in Figure 2.

Under all environmental conditions, the initial growth of red alder was substantially greater than that of Douglas-fir, and dominance of alder was assured when alder and Douglas-fir were established simultaneously on the same site. Moreover, Douglas-fir could not be expected to maintain a position at least of codominance with red alder unless it was established 3 to 8 years before the alder (Table 1); the adjustment period was as great as 10 years in individual stands. The most important factors influencing the advantage of alder seemed to be related to moisture regime; that is, wet bottoms and steep slopes with active seepage favored red alder more than Douglas-fir, even though the absolute growth of Douglas-fir on moist sites was greater than on drier slopes. The influence of degree of slope and general moisture regime is illustrated in Figure 3.

Comparison of adjustment periods between regions as affected by the various environmental parameters shows that steep slopes had a different
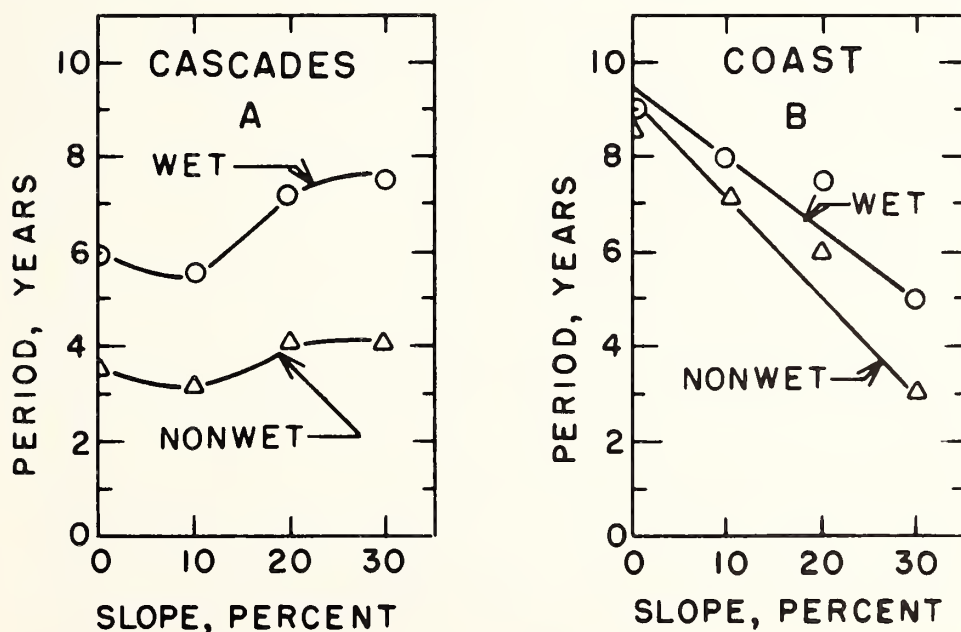
Figure 3. Relation between adjustment period and slope in the Cascades and Coast regions. Sampling for the valley slope of the Coast Ranges was incomplete, and these data are not presented graphically.

effect on the adjustment period in the Cascade Range than in the Coast Ranges. This difference may have been attributable to greater amounts of seepage on steep slopes in the Cascade Range than on the low sandstone topography of the Coast Ranges. Because of the more xeric conditions in the Cascade Range, the need for additional moisture from adjacent land is understandable though this explanation is still speculative.

Perhaps the most important finding about the adjustment period is that the range of time did not vary substantially with location and parent material; the range was from 3 to 8 years at each location. The ages at which Douglas-fir height would be expected to equal that of red alder under open-grown conditions when established at the same time and the adjustment period needed to establish dominance of Douglas-fir from the outset are illustrated in Table 1.

TABLE 1. Adjustment periods, and approximate age-height relationships in unadjusted stands after which Douglas-fir retains dominance in three locations.

Location	Wet			Nonwet		
	Adjust-ment years	Unadjusted point of dominance		Adjust-ment years	Unadjusted point of dominance	
		Age	Height		Age	Height
			Feet			*Feet*
Cascades	7	44	81	4	25	40
Coast Ranges, valley slope	8	40	92	4	33	82
Coastal slope	8	40	100	6	35	86

Note in Table 1 that on nonwet sites an advantage of 4 years is sufficient to prevent 25-35 years of partial or complete suppression, with a good chance for conifer mortality even on sites where Douglas-fir can best compete with red alder. Eventual emergence of Douglas-fir would be contingent on its ability to grow at open-grown rates while being suppressed, which is an unlikely phenomenon for Douglas-fir, but perhaps possible for more tolerant species. The adjustment periods are greatest on the wettest sites, with unadjusted Douglas-fir being dominated by as much as 25 feet. Even tolerant species may be unable to survive this degree of suppression. Observations of suppressed Douglas-fir indicated that growth of overtopped trees decreased rapidly after canopy closure, with mortality usually following closure by not more than 5-7 years. No Douglas-fir was able to maintain a normal growth habit after falling into lower than a codominant position;

only one fir was able to maintain codominance in a medium-stocked stand of red alder on a good site for 14 years.

Nitrogen accretion.—Evidence was strong that alder fixes significant amounts of nitrogen. Within the limitations of sampling precision in attempting to reconstruct accretions to unknown initial nitrogen levels, there was a strong trend of increases in total nitrogen in stands of increasing age. Based on stands between 2 and 15 years of age, which is the range of ages for which sampling was conducted with reasonable confidence in the initial conditions, there appears to have been an annual increase of some 320 kg per hectare in the biomass and top 60 centimeters of soil (Fig. 4). Differences were difficult to detect because of the large amounts of nitrogen in all
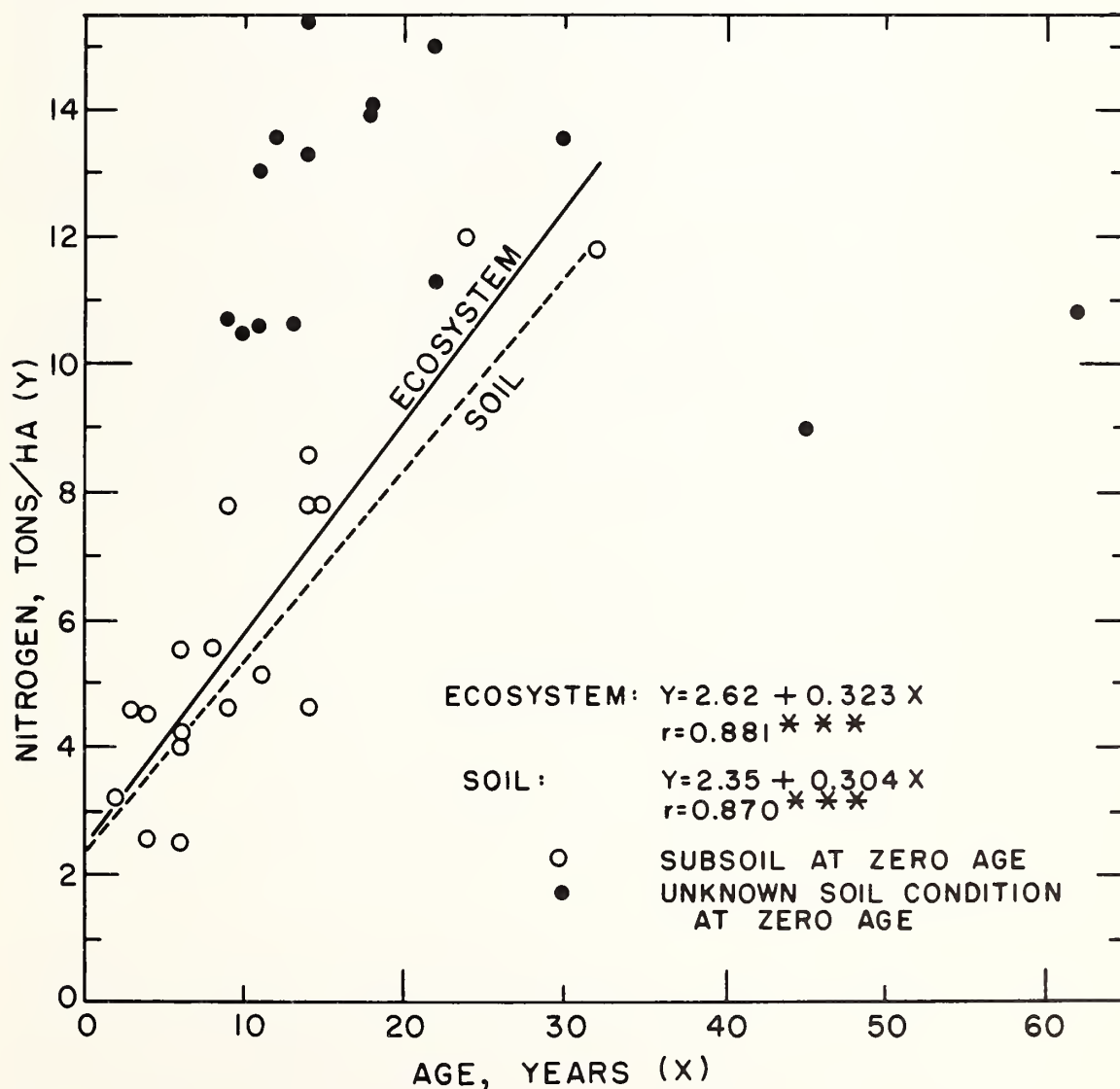
Figure 4. Accumulation of nitrogen in red alder ecosystems and soils. Regression lines are based only on soils scarified at the time of stand origin.

sites supporting alder more than 10 years of age and the small percentages of change and heterogeneity of sampling material. It is sufficient to observe, however, that all stands (with the exception of one observation within one stand) more than 15 years of age were growing on sites with between 8,000 and 15,000 kg per hectare of nitrogen in the top 60 cm of soil plus litter. Moreover, there was no evidence of further accretion once these high levels had been reached.

Physical conditions in surface soils under red alder showed distinct changes with increasing stand age. The accumulation of litter, which appeared to be balanced by breakdown at the age of 7 years, indicated a strong tendency for bulk density of soil to decrease as the organic material was incorporated. This tendency extended to a depth of 60 cm or more. Some nodules were found at depths of 30-60 cm in highly compacted soils, and compaction, in general, did not appear to greatly restrict rooting of alder. This sampling did not include soil in the Cascade Range, however, and estimates of fixation in that region cannot be extrapolated with confidence. Because of the poorer performance of alder in that region, fixation would not likely be greater than in the Coast Ranges; certainly accumulations of nitrogen in the biomass would be less in the Cascade Range, but this represents a small percentage of the total nitrogen on the site.

Discussion and Conclusions

Red alder is capable of suppressing Douglas-fir almost to its exclusion, when the two species are established at the same time on the same location. The ability of alder to dominate early stages in secondary succession appears to depend on its ability to become established, rather than its adaptation to specific sites because of its growth. The general occurrence of Douglas-fir in localities where alder regeneration is abundant might be construed to mean that there are some exceptions to the above picture of ubiquitous alder dominance.

Throughout this investigation, we noted that density of alder regeneration was related to the degree of scarification and relative duration of summer drought. Disturbances that favored dense stands were almost invariably in the form of logging roads, landings, and other forms of localized deep scarification. In agreement with McVean (1956), almost any amount of litter or other organic layer on the soil surface apparently created microenvironments more droughty than alder seedlings could tolerate. This condition was more pronounced on south slopes than on other aspects, and increased with increasing distance from the coast. Relative humidity in the vicinity of germinating seeds was cited by McVean (1956) as responsible for similar distribution of black alder in Europe.

Failure of red alder to become established on nonscarified soil has important implications for development of Douglas-fir. Seldom is scarification complete on fresh logging operations, and the size of unscarified spots determines the area in which Douglas-fir can become established with influence of alder restricted to side shade. The ultimate success of Douglas-fir is inversely related to the height-growth advantage of the alder and is directly related to the size of opening in which it is growing. Moreover, the concept of adjust-

ment period may be used to describe a particular site in terms of the degree of advantage needed for Douglas-fir to become established on alder sites, or conversely, as an inverse measure of the chances of success of Douglas-fir when the two species are established concurrently. Since an array of undisturbed areas nearly always exists on logged sites, there is a strong likelihood that Douglas-fir will eventually reach dominance on the larger openings in stands dominated by alder without serious suppression. The theory that Douglas-fir will succeed red alder by persisting until dominance is reached is refuted by this evidence. Notwithstanding, few mature Douglas-fir trees are required to form a forest. By the age of 80 years, at which time red alder approaches senescence, a small number of Douglas-fir trees per acre will form the dominant component of a stand that has arisen from dense alder with a few isolated coniferous saplings in openings. The economic value of the few conifers is far greater than that of the alder, hence it is not surprising that considerable significance is attached to their emergence. Because success of Douglas-fir is the direct result of longevity and continued growth over a long period, adoption of short rotations and cutting cycles will reduce greatly the fir's chances of forming a major component of the forest if alder is allowed to develop naturally.

The role of alder in soil development where surface soil is removed has been demonstrated clearly, both in nitrogen fixation and in the additional improvement of soil structure. Three important qualifications condition interpretation of this role in the long-term ecology of forests: (1) Some nitrogen is lost through burning on cutover lands, but most of the losses from scarification are piled up nearby, well within the reach of root systems of mature trees; (2) the very occurrence of dense stands of alder is sufficient to preclude development of species that might utilize large amounts of nitrogen; and (3) the accumulation of nitrogen in pure stands of alder almost ceases well before the alder is mature, presumably because fixation follows an inverse ratio to the nitrogen available in the soil.

In conclusion, alder clearly plays a variable role in determination of secondary forest succession. Where establishment is difficult, stands of high density may be rare and Douglas-fir may occur in sufficient small openings to form a complete stand without serious suppression. Under these circumstances, occurrence of the alder may increase soil nitrogen to the advantage of the coniferous cover. As conditions for establishment of alder improve, almost regardless of growing conditions after germination, the chances for Douglas-fir survival are restricted greatly, although some trees will probably occur in unscarified openings to form eventually a scattered stand with shrub understory. On the wettest sites, alder may develop even on unscarified soil, may dominate all conifers, and is likely to be succeeded eventually by shrubs almost to the exclusion of tree species. Presumably, the tolerant conifers would develop eventually as scattered individuals that have utilized local disturbances for establishment. Under these circumstances, the same species that would eventually replace Douglas-fir in the climax forest may also succeed the shrub subclimax, but Douglas-fir will not be an important part of the successional sequence.

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Comparison of vegetation in adjacent alder, conifer, and mixed alder-conifer communities II. Epiphytic, epixylic, and epilithic cryptogams

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Abstract

Epiphytic and epixylic cryptogams were compared in adjacent red alder, conifer, and mixed alder-conifer communities. Twenty-four epiphytic species were encountered. Red alder was a more favorable host than Douglas-fir or Sitka spruce in terms of number of epiphytic cryptogams and their frequency and coverage. Mosses were represented best on tree bases; liverworts, on midportions of tree trunks; and lichens, on upper trunks and in crowns. Thirteen species of epixylic cryptogams were encountered during sampling of rotten logs.

Relatively few data are available on the occurrence and abundance of cryptogams in forest communities of the Pacific Northwest. However, cryptogams are often an important part of these ecosystems, especially in the coastal "fog belt." To provide a more complete picture of the vegetation of adjacent red alder *(alnus rubra)*, conifer (mostly Douglas-fir *(Pseudotsuga menziesii)*), and mixed alder-conifer communities previously described (Franklin and Pechanec, 1968), an analysis and comparison of epiphytic, epixylic, and epilithic cryptogams was conducted. The results are presented in this report.

Methods

In each stand, a 2- by 5-dm-plot frame was used to obtain frequency and coverage figures for epiphytic cryptogams. Two basal levels, from a height of 0 to 5 dm and from 5 to 10 dm above ground, were examined on trunks of two or three standing trees of each species in each stand.

Data on cryptogamic coverage of lower trunks (over 1 meter above ground line), upper trunks, and crowns were obtained from two felled trees

each of red alder and Douglas-fir and from one small Sitka spruce (*Picea sitchensis*). Felled trees were growing in the mixed stand of red alder and conifer. The Douglas-fir were 18 inches in diameter at the stump and about 70 feet tall; felled red alder were approximately 15 inches in diameter and 60 feet tall.

Frequency and coverage of epixylic cryptogams were determined by examining ten 2- by 5-dm plots located on randomly selected rotting logs in each of the three stands. A single rock in the pure alder stand, covered with distinctive epilithic crytogams and not ground species, was studied by use of five 2- by 5-dm plots.

Estimates of coverage and calculation of frequency and coverage follow the methods outlined by Daubenmire (1959).

Results

Epiphytic crytogams (hereafter called "epiphytes" in this paper) can be divided into four groups (Table 1). The first group, composed of two liverworts, three mosses, and two lichens, was found on all three tree species (red alder, Douglas-fir, Sitka spruce). Both liverworts, *Frullania franciscana* and *Radula bolanderi,* extended into the upper trunk region. Of the mosses, *Eurhynchium oreganum* extended onto the lower trunk and *Isothecium spiculiferum* extended onto the upper trunk. The third moss, *Ulota obtusiuscula,* was restricted to trunk and crown. *Lecanora subfusca,* one of the two lichens, extended from tree base onto the upper trunk on alder, but was on the lower trunk of all three tree species. *Cetraria ciliaris,* the other lichen, was found only on the upper trunk and crown.

The second group of epiphytes was found on alder and spruce and was composed of one liverwort, one moss, and three lichens. The liverwort, *Porella navicularis,* and one lichen, *Lepraria* sp., occurred from base to upper trunk and were most abundant on alder. The moss, *Neckera douglasii,* occurred only on the trunk. Of the other two lichens, *Cladonia coniocraea* was restricted to the lower trunk, whereas *Usnea glabrescens* occurred on both trunk and crown.

The third group composed of three epiphytes, was found on alder and Douglas-fir. All three, a moss, *Orthotrichum lyellii,* and two lichens, *Pertusaria* sp. and *Parmelia enteromorpha,* were trunk and crown species.

The fourth group of epiphytes was found only on alder. Two liverworts, two mosses, and five lichens comprised this group. The liverworts, *Calypogeia muelleriana* and *Metzgeria conjugata,* the mosses, *Eurhynchium stokesii* and *Plagiothecium undulatum,* and the lichen, *Graphis scripta,* occurred only at the lowest (0 to 5 dm) level, but the lichen, *Mycoblastus sanguinarius,* extended onto the upper trunk. Three lichens, *Microthelia micula, Parmelia sulcata,* and *Menegazzia terebrata,* were trunk and crown species.

No epiphyte was found which occurred only on the conifers.

The number of species of epiphytes found at different heights on the three tree species is shown in table 2. On alder, number of epiphytes dropped from the first to the second 5 dm of height. An increase of species on the lower trunk (above 1 m), the richest level on the alder, was followed by a decrease

TABLE 1. Frequency and percent coverage of epiphytes growing on red alder, Douglas-fir, and Sitka spruce, showing distribution at different heights (frequency/coverage)

Species and group[1]		Base of tree						Trunk of tree						Crown	
		0- to 5-dm height			5- to 10-dm height			Lower			Upper				
		Red alder	Douglas-fir	Sitka spruce	Red alder	Douglas-fir	Sitka spruce	Red alder	Douglas-fir	Sitka spruce	Red alder	Douglas-fir	Sitka spruce	Red alder	Douglas-fir
On all three tree species:															
Eurhynchium oreganum	(M)	100/38	100/22	80/21	100/5	100/18	20/3	7/4	20/4	80/36	46/4				
Isothecium spiculiferum	(M)	100/38	40/6	80/40	100/39	40/8	80/4	80/41	80/8	30/14	66/12				
Frullania franciscana	(H)	40/4			60/28	80/7	20/3	80/25	100/30	10/2	27/2	100/43			
Lecanora subfusca	(L)	20/3			20/.5			23/3	10/2		9/1				
Radula bolanderi	(H)	20/.5				60/4		13/2	20/.5	10/2	20/2	40/2			
Ulota obtusiuscula	(M)							13/3			3/1	30/.8	10/.8	20/.5	
Cetraria ciliaris	(L)						20/.5			10/2				5/1	40/6
On red alder and Sitka spruce:															
Porella navicularis	(H)	40/1			20/3			20/3		20/2	50/7				
Lepraria sp.	(L)	20/.5			80/7			7/1		20/.5	7/1				
Cladonia coniocraea	(L)	20/.5		20/.5	20/.5		20/.5	3/.1		20/.5					
Neckera douglasii	(M)							23/2		10/2	20/.5				
Usnea glabrescens	(L)							3/.1		10/2	3/.1			25/.6	
On red alder and Douglas-fir:															
Orthotrichum lyellii	(M)							43/8	60/3		43/8	50/2		25/.6	
Pertusaria sp.	(L)							10/1	50/21		100/36	70/2			80/2
Parmelia enteromorpha	(L)										50/12			85/16	100/24
On red alder only:															
Microthelia micula	(L)							7/1			7/5			10/.2	
Parmelia sulcata	(L)										7/6			3/.5	
Menegazzia terebrata	(L)							3/.1						15/2	
Mycoblastus sanguinarius	(L)	20/.5			20/.5						3/.1				
Eurhynchium stokesii	(M)	60/2									3/.1				
Plagiothecium undulatum	(M)	40/1													
Graphis scripta	(L)	20/.5													
Calypogeia muelleriana	(H)	20/.5													
Metzgeria conjugata	(H)	20/.5													

[1]*M indicates moss; H, liverwort (hepatic); and L, lichen.*

TABLE 2. Numbers of epiphytes by group, level on host, and host[1]

Level on tree	Red alder				Douglas-fir				Sitka spruce			
	H	M	L	Total	H	M	L	Total	H	M	L	Total
0 to 5 dm	6	4	5	15	0	2	0	2	0	2	0	2
5 to 10 dm	2	2	3	7	2	2	1	5	2	2	1	5
Lower trunk	3	5	8	16	2	3	2	7	3	2	5	10
Upper trunk	3	4	5	12	2	2	2	6	0	1	0	1
Crown	0	2	5	7	0	0	3	3	--	--	--	--

[1]*H indicates liverwort (hepatic); M, moss; and L, lichen.*

on the upper trunk and crown. On both conifers, an increase in number of epiphytes occurred in the second 5 dm of height. As on alder, the lower trunk had the highest number of species with a decrease in upper trunk and crown. A tendency for the proportion of lichen species to increase from lower trunk to upper trunk to crown was evident on the alder and Douglas-fir.

On alder there was a decrease in frequency (but not coverage) of epiphytes from the first to second 5 dm (Table 3) just as there was in number of species (Table 2). On Douglas-fir the increase in frequency and coverage of epiphytes at 5- to 10-dm level matched the increase in number of species. At least part of the greater frequency and coverage totals for epiphytes on alder (Table 3) was due to a greater number of species. This was especially true in the 0- to 5-dm level where 14 of the 24 epiphytes recorded in this study were present. On Douglas-fir only two and on Sitka spruce only four species of the total 24 epiphytes were recorded in the 0- to 5-dm level. The high coverage at this level on the Sitka spruce was due almost entirely to a mantling of *Isothecium spiculiferum* (Fig. 1).

Coverage of all epiphytes taken together was greatest on the lower portion of the trunk on red alder and on the upper trunk on Douglas-fir (Table 3). The crown appears less favorable for development of epiphytes than other positions on the bole.

Optimum levels on the trees for development of mosses, lichens and liverworts differ (Table 4). Mosses have their best representation at the base of the trees, liverworts on midportions of the boles, and lichens on the upper trunks and crowns.

TABLE 3. Summation of frequency and coverage percent of individual epiphytes by level on host and host tree species

Level on tree	Red alder		Douglas-fir		Sitka spruce	
	Frequency	*Percent coverage*	*Frequency*	*Percent coverage*	*Frequency*	*Percent coverage*
0 to 5 dm	540	52	140	28	200	62
5 to 10 dm	420	83	280	36	160	10
Lower trunk	344	93	340	68	220	56
Upper trunk	360	51	390	86	10	1
Crown	185	21	220	32	--	--
Totals	1,849	298	1,370	250	590	129

Figure 1. *Isothecium spiculiferum* **was particularly abundant on suppressed Sitka spruce saplings.**

TABLE 4. Summation of frequency and coverage percent by kind of epiphyte and level on tree[1]

Level on tree	Liverwort		Moss		Lichen		All	
	Frequency	Percent coverage	Frequency	Percent coverage	Frequency	Percent coverage	Frequency	Percent coverage
0-5 dm	160	7	600	168	120	6	880	180
5-10 dm	260	46	440	77	160	9	860	131
Lower trunk	296	77	416	109	186	32	898	217
Upper trunk	265	65	222	18	277	54	760	138
Crown	None		45	1	363	51	405	52

[1]Includes data from all three tree species.

Composition and coverage of epiphytes differ on red alder growing in the mixed and pure alder stands (Table 5). *Eurhynchium stokesii, Mycoblastus sanguinarius, Plagiothecium undulatum, Orthotrichum lyellii, Graphis scripta, Lecanora subfusca, Radula bolanderi,* and *Calypogeia muelleriana* are found on alder at 0- to 5-dm or 5- to 10-dm levels, or both, in the pure stand, but not at these levels on alders growing in the mixed stand. Apparently these eight species prefer alder under conditions found in the pure stand. Two liverworts, *Frullania franciscana* and *Porella navicularis,* are more frequent at the 5- to 10-dm level on alder in the pure stand; coverage is less for *Frullania,* but more for *Porella* than on alder growing in the mixed stand. *Metzgeria conjugata,* a liverwort, and *Cladonia coniocraea,* a lichen, are present on alder in the mixed stand at the 0- to 5-dm level and the latter also at 5- to 10-dm level, but not at these levels in the pure alder stand. Two mosses, *Isothecium spiculiferum* and *Eurhynchium oreganum,* show a greater frequency in the mixed stand with a higher coverage for the former, but equal coverage in in the two stands for the latter species (Fig. 2).

Thirteen species of epixylic cryptogams were recorded (Table 6). Two mosses, *Tetraphis* sp. and *Mnium glabrescens,* and the liverwort, *Lepidozia reptans,* were found on rotten wood only in the pure alder stand. The moss, *Plagiothecium denticulatum,* and two liverworts, *Scapania Bolanderi* and *Riccardia latifrons,* were found on rotten wood only in the pure conifer stand. The moss, *Eurhynchium stokesii,* occurred as an epixylic cryptogam in the mixed alder-conifer stand. *Rhytidiadelphus loreus,* a moss, was found in both the pure alder and mixed stands; *Calypogeia muelleriana,* a liverwort, occurred on rotten wood in both pure alder and conifer stands; and *Isothecium spiculiferum* in both conifer and mixed stands. Only three out of the 13 epixylics, all mosses, were found in all three stands — *Eurhynchium oreganum* (Fig. 3), *Plagiothecium undulatum,* and *Dicranum fuscescens.*

TABLE 5. A comparison of frequency and percent coverage of epiphytes found on the base of red alders when growing in pure and mixed stands[1]

Epiphyte		0- to 5-dm height				5- to 10-dm height			
		Pure stand		Mixed stand		Pure stand		Mixed stand	
		Frequency	*Percent coverage*	*Frequency*	*Percent coverage*	*Frequency*	*Percent coverage*	*Frequency*	*Percent coverage*
Eurhynchium oreganum	(M)	100	40	100	38	20	3	100	5
Isothecium spiculiferum	(M)	60	9	100	38	60	11	100	39
Metzgeria conjugata	(H)	0	0	20	.5	0	0	0	0
Cladonia coniocraea	(L)	0	0	20	.5	0	0	20	.5
Frullania franciscana	(H)	40	1	40	4	100	20	60	28
Porella navicularis	(H)	40	4	40	1	60	11	20	3
Lepraria sp.	(L)	0	0	20	.5	20	.5	80	7
Eurhynchium stokesii	(M)	60	2	0	0	0	0	0	0
Mycoblastus sanguinarius	(L)	20	.5	0	0	20	.5	0	0
Plagiothecium undulatum	(M)	40	1	0	0	0	0	0	0
Orthotrichum lyellii	(M)	0	0	0	0	20	.5	0	0
Graphis scripta	(L)	20	.5	0	0	0	0	0	0
Lecanora subfusca	(L)	20	.5	0	0	20	.5	0	0
Radula bolanderi	(H)	20	.5	0	0	0	0	0	0
Calypogeia muelleriana	(H)	20	.5	0	0	0	0	0	0

[1] *M indicates moss; H, liverwort; and L, lichen.*

Epilithic cryptogams found on a boulder in the pure alder stand and their frequency and percent coverage are: *Eurhynchium oreganum,* 60/2; *Rhytidiadelphus loreus,* 60/32; *Claopodium crispifolium,* 20/8; and *Peltigera aphthosa,* 100/40.

Discussion

The Cascade Head alder-conifer stands are relatively rich in cryptogamic species considering the small area they occupy. A total of 38 species was found growing on different habitats—16 mosses, 8 liverworts, and 14 lichens (Table 7).[1] This number is, however, considerably less than Sharpe (1956) reports for red alder and conifer stands in the Olympic rain forest region. Five of 16 liverworts, eight of 27 mosses, and eight of 28 lichens Sharpe found in Olympic red alder stands were present at Cascade Head. About the same proportion of cryptogamic species holds when Sharpe's data for

[1] *Data for ground-dwelling cryptogams from Franklin and Pechanec (1968).*

Figure 2. *Isothecium spiculiferum* and *Parmelia enteromorpha* dominate on the lower trunk of this red alder.

TABLE 6. Frequency and percent coverage of epixylic cryptogams found on well-rotted logs in the three stands[1]

Epixylic cryptogams		Alder		Conifer		Mixed	
		Frequency	Percent coverage	Frequency	Percent coverage	Frequency	Percent coverage
Eurhynchium oreganum	(M)	80	38	60	31	100	68
Plagiothecium undulatum	(M)	70	19	40	1	30	5
Lepidozia reptans	(H)	30	6				
Dicranum fuscescens	(M)	30	2	10	.2	10	.2
Tetraphis sp.	(M)	10	2				
Mnium glabrescens	(M)	10	.2				
Calypogeia muelleriana	(H)	10	2	50	24		
Rhytidiadelphus loreus	(M)	10	6			30	.2
Scapania bolanderi	(H)			60	8		
Isothecium spiculiferum	(M)			20	9	20	.5
Plagiothecium denticulatum	(M)			10	4		
Riccardia latifrons	(H)			10	.2		
Eurhynchium stokesii	(M)					20	4

[1] M indicates moss and H, liverwort.

Figure 3. *Eurhynchium oreganum* was an abundant moss on basal portions of trees and on rotting logs as well as on the ground.

Douglas-fir and Sitka spruce stands are compared with the Cascade Head conifer data. Some of the species listed by Sharpe (1956) which were not found in the Cascade Head alder-conifer stands are *Ptilidium californicum* (a liverwort), several species of *Lobaria* and *Peltigera* (lichens), and the mosses, *Hypnum circinale* and *Mnium menziesii*. There are also many more species of the lichen genera *Cetraria* and *Parmelia* in the stands on the Olympic Peninsula.

The differences between the Cascade Head and Olympic data are at least partially related to (1) Sharpe's larger sample covering a much larger geographic area and (2) a more favorable (moister) climatic regime on the west side of the Olympic Peninsula. The importance of climate has been shown by Coleman et al. (1956). They compared distributions of host plants and epiphytes at 20 different locations on the Olympic Peninsula and found definite host-location interactions—certain hosts did not bear the same numbers of species of epiphytes at all locations. This strongly suggests that

variation in climatic factors (e.g., mean annual rainfall and short-time variations in water supply at the epiphyte's surface) affects kinds and abundance of epiphytes on a given host plant.

Red alder is a more favorable host for epiphytes than either Douglas-fir or Sitka spruce (Tables 2 and 3). There are consistently more epiphytic species present at all levels on red alder trees and, except in upper trunk and crown, a greater frequency and coverage of epiphytes. This is consistent with the findings of Coleman et al. (1956) that red alder was the most receptive host of 43 epiphytes they studied. They felt potential trunk diameter, tree height, and bark characteristics might be related to host receptivity. However, of these three characteristics at Cascade Head, only the bark character differed between red alder and conifers. These bark differences certainly do account for much of the superior epiphytic coverage on alder at Cascade Head. Red alder bark, in contrast to that of Douglas-fir and Sitka spruce, is smoother, softer, and spongier, and does not scale off.

The differing optimum levels on the tree for development of epiphytic mosses, lichens, and liverworts (Table 4) are undoubtedly related to both (1) competition and (2) physiological differences between individual species and the three major groups of epiphytes. The problem of competition between epiphytic species is obvious. On portions of host plants where two species are equally capable of growing physiologically, the more robust will tend to crowd the other out.

Each species of cryptogams does, of course, have its physiological limits; namely, (1) the amount of exposure it can tolerate as determined by moisture stresses and (2) the amount of shading it can stand as determined by compensation point. Patterson (1964) emphasized the first of these limits when he pointed out that bryophytic species will grow only in microhabitats where desiccation does not surpass a critical level for a critical length of time. Hosokawa et al. (1964) stressed the second of these physiological limits when they grouped corticolous mosses and lichens into stump, trunk, and crown species on the basis of daily compensation periods. Crown species, they said, cannot grow much below the crown nor trunk species much below the trunk. Stump species, then, are those that can grow where the higher level species cannot grow because of the limit of low daily compensation periods.

We can conclude that the upper limits for epiphytes are generally determined by moisture relations and the lower limits by light relations, including competition for light among the various epiphytic species. Distribution patterns found on red alder and conifers at Cascade Head are readily explained in this fashion. For example, the relative paucity of liverworts at the 0- to 5-dm level is likely due to competition from robust mosses such as *Eurhynchium oreganum* and *Isothecium spiculiferum*. Similarly, the lichens, with their less exacting moisture requirements, find the tree crowns a favorable habitat, away from smothering mosses and liverworts.

TABLE 7. Check list of cryptogamic species present in the Cascade Head alder-conifer stands by the habitats on which they were found[1]

Group and species		Habitat							
			Living trees						
		Base		Trunk		Crown			
	Ground	Alder	Conifer	Alder	Conifer	Alder	Conifer	Rotten logs	Rocks
Mosses:									
Campylium sp.	X								
Claopodium crispifolium (Hook.) Ren. & Card.									X
Dicranum fuscescens Turn.									
Eurhynchium oreganum (Sull.) Jaeg.	X	X	X		X			X	
Eurhynchium stokesii (Turn.) B.S.G.	X							X	X
Isothecium spiculiferum (Mitt.) Ren. & Card.	X	X	X		X			X	
Mnium glabrescens Kindb.								X	
Mnium insigne Mitt.	X								
Mnium punctatum Hedw.	X								
Neckera douglasii Hook.	X			X	X				
Orthotrichum lyellii Hook. & Tayl.				X	X		X		
Plagiothecium denticulatum (Hedw.) B.S.G.	X							X	
Plagiothecium undulatum (Hedw.) B.S.G.	X		X					X	
Rhytidiadelphus loreus (Hedw.) Warnst.	X							X	X
Tetraphis sp.								X	
Ulota obtusiuscula C. Mull. & Kindb.				X	X		X		
Liverworts:									
Calypogeia muelleriana (Schiffn.) K. Mueller		X						X	
Frullania franciscana Howe		X	X		X				
Lepidozia reptans (L.) Dum.				X				X	
Metzgeria conjugata Lindb.		X							
Porella navicularis (J. & L.) Lindb.		X		X	X				

TABLE 7. Continued

Group and species	Ground	Base Alder	Base Conifer	Trunk Alder	Trunk Conifer	Crown Alder	Crown Conifer	Rotten logs	Rocks
Radula bolanderi Gottsche		X	X	X	X				
Riccardia latifrons Lindb.								X	
Scapania bolanderi Aust.	X							X	
Lichens:									
Cetraria ciliaris Ach.		X		X	X	X	X		
Cladonia coniocraea (Flk.) Spreng. f. *coniocraea*		X	X	X	X				
Graphis scripta (L.) Ach.		X		X					
Lecanora subfusca (L.) Ach.		X		X	X				
Lepraria sp.		X		X	X				
Menegazzia terebrata (Hoofm.) Mass.				X		X			
Microthelia micula Flot.				X		X			
Mycoblastus sanguinarius (L.) Norm.		X		X					
Ochrolechia frigida (DR.) Lynge				X					
Parmelia enteromorpha Ach.				X	X	X	X		
Parmelia sulcata Tayl.				X		X			
Peltigera aphthosa L. Willd.									X
Pertusaria sp.				X	X		X		
Usnea glabrescens ssp. *glabrescens* Mot.				X	X	X			

¹ *Data for ground-dwelling cryptogams from Franklin and Pechanec (1968).*

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First-season growth of red alder seedlings under gradients in solar radiation

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Abstract

Red alder (Alnus rubra *Bong.) seedlings were grown on mineral soil near the Oregon coast under a conifer stand thinned to provide gradients in canopy density. First-season survival was one seedling per 31 viable seeds sown, indicating a low efficiency for alder establishment compared with conifers under similar conditions. Only a small part of variation in growth was associated with radiation reaching the forest floor.*

Introduction

General silvicultural practice in coastal areas of Oregon and Washington is to clearcut mature timber stands and establish tree seedlings in the open. This practice favors red alder which soon overtops and suppresses slower starting Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). A recent trend is to use the shelterwood system and establish seedlings under the shade and protection of part of the mature stand. With more information on shading requirements for seedlings, it may be possible to manipulate a shelterwood canopy to provide radiation levels favorable or unfavorable to red alder, depending on management objectives.

Objectives here were to measure some relationships between solar radiation and establishment of red alder seedlings on mineral soil under a mature 118-year-old spruce-hemlock-fir stand 6.0 miles from the Pacific Ocean and 3.5 miles northeast of Otis, Oregon. Elevation of the study area ranges from 750 to 1,000 feet above sea level and topography is gentle, north facing, with average slope about 10 percent.

Methods

The timber stand was thinned in four strips, each providing a gradient in canopy density and solar radiation reaching the forest floor. The strips were 1,650 to 2,375 feet long and 330 feet or more wide. Canopy density decreased from north to south on two strips and south to north on the other

two (Fig. 1). One-milacre plots were established at about 90-foot intervals down the center of each strip for a total of 82 plots, and five supplemental plots were established in a nearby stand opening. Understory vegetation was removed from all plots by tractor scarification.

Seedspots were prepared by imbedding 28-cm-diameter circular screens into the mineral soil with about 2.5 cm protruding above the surface. The screens provided a fence around the seedspots to let water out but keep seed in. Twenty-four previously stratified red alder seed from local seed trees were sown April 15 to 21, 1965, in each seedspot and covered with about 3 mm of mineral soil. Seedspots were covered with 4-mesh hardware cloth for 1 month to keep out rodents. Seed viability tests in a growth chamber set at 25° C for day and 17° C for night temperatures had given 58-percent viability, indicating an average of 14 viable seed were sown per seedspot.

Seedling counts were made May 20 to 24, June 8 to 9, June 30 to July 2, August 8 to 11, and September 22, 1965. In November, all seedlings were carefully lifted, soil washed from roots, top height and root length measured, and oven-dry weight of tops and roots determined. Foliage was present on the seedlings at lifting and was included in the weights.

Solar radiation was measured photochemically using a solution of anthracene in benzene in borosilicate glass vials (Dore, 1958; Rediske, Nicholson,

Figure 1. Moderate timber overstory along truck road with dense overstory in the left background.

and Staebler, 1963). Vials were exposed at ground level simultaneously on all plots and in a stand opening beside a Moll Gorczynski solarimeter sensitive to wave lengths from 280 to 3,000 nanometers. This procedure permitted correlation of photochemical determinations with a standard radiation measurement and comparison of radiation under the forest canopy and in the open. Radiation was measured on a clear day, August 5, 1965; a partly cloudy day, August 26; and during cloudy weather from September 8 to 10. Measurements thus sampled different kinds of weather conditions and integrated radiation over sufficient time that effects of sunspots were included.

A supplemental study of alder seedling growth at various radiation levels was made utilizing 100 first-year seedlings growing at 64 locations on mineral soil along tractor roads under the same shelterwood stand. The seedlings originated from natural seedfall and were growing in a wide range of radiation levels on various aspects and slopes. Radiation was measured beside the seedlings at about 10 cm above the ground level using vials suspended with a wire attached at the base of the opaque cap. Radiation was measured October 13 to 18, 1965 during an overcast period. After radiation measurements, seedlings were clipped just below ground level and measured for height.

Statistical relations between radiation levels under the forest canopy and seedling survival and seedling growth were evaluated by regression analyses.

Results

Establishment of red alder seedlings in the prepared seedspots under the forest canopy was low with average number of live seedlings per seedspot reaching a peak of only 0.80 by August 15, then declining to an average of about 0.45 per seedspot at the end of the season (Fig. 2). A significant quadratic regression coefficient (0.05 level) indicated that significant mortality occurred during the season. Only 38 seedlings on 16 plots survived to be measured at the end of the season. This was one seedling per 31 viable seed sown. No seedlings became established in the stand opening.

Effect of solar radiation on seedling establishment was evaluated by a regression analysis relating number of seedlings per seedspot at the end of the growing season to radiation. No significant relationship was found.

The 38 red alder seedlings that survived the growing season were small in size. Average weights and dimensions of seedspot seedlings were:

Measurement	Average alder seedling
Total weight	22.1 mg
Top weight	10.7 mg
Root weight	11.4 mg
Top-root ratio (weight basis)	1.0
Total length	72.1 mm
Height	21.4 mm
Root length	50.7 mm
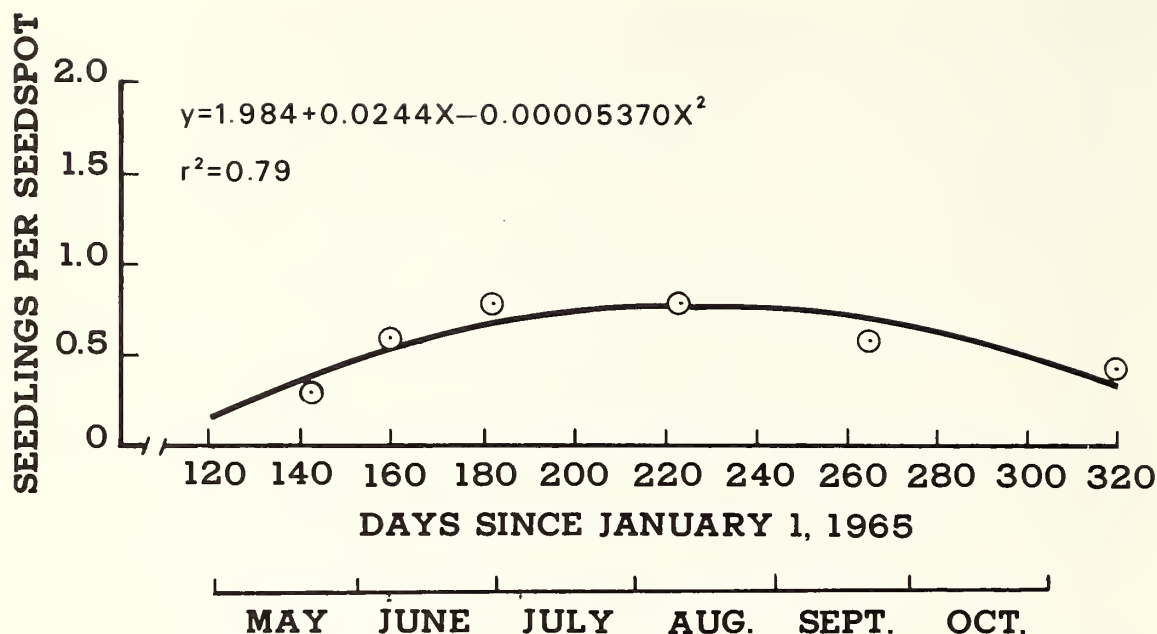
Figure 2. Average number of live red alder seedlings per seedspot during 1965.

Regressions were calculated relating average seedling weight and dimensions at end of growing season to average daily solar radiation, and the only significant relationships found were for total length and root length. Both increased significantly with radiation (0.01 level). Forty percent of the variation in total length and 53 percent of the variation in root length was associated with radiation (Fig. 3).

Height of the natural alder seedlings growing along tractor roads increased with increased average daily solar radiation, reaching a maximum at 39 percent of full sunlight, then decreased as average radiation became greater (Fig. 4). Solar radiation accounted for 26 percent of the variation in seedling height, and curvilinearity was significant at the 0.01 level. Seedlings averaged 45.8 mm in height.

Discussion

The seed-to-seedling ratio of 31 viable red alder seed to one established seedling indicates a low efficiency for alder establishment under a forest canopy. The ratio for native conifers under similar conditions was much better, averaging about 6 to 1 (Ruth, 1967). Red alder generally prefers a mineral soil seedbed (Worthington, Ruth, and Matson, 1962), and this preference was evident under the shelterwood canopy where seedlings from natural seedfall were found only on mineral soil. If an objective is to encourage red alder, increased exposure of mineral soil may help; if it is to discourage alder, minimal disturbance of the forest floor seems indicated. Since western hemlock and Sitka spruce readily germinate and grow on organic seedbeds (Ruth, 1965), reduced disturbance of the natural forest floor may

have a differential effect favoring these conifers. There were no alder seed trees in the shelterwood area, so observation of natural alder seedlings along tractor roads indicated some capacity for seed to drift in from nearby stands. Elimination of such seed sources also should reduce alder establishment.

Survival of only 38 alder seedlings on the milacre plots left only a small sample for measurement of radiation effects, and about all that can be said with certainty is that first-year seedlings showed a surprising tolerance of shade. One seedling survived the season under an average radiation of only 7.2 langleys per day, or only 2.3 percent of radiation in the open. The data indicated no significant relationship between number of seedlings established under the forest canopy and radiation. Whether this result was due to the small sample or to minor effects of radiation relative to other variables must
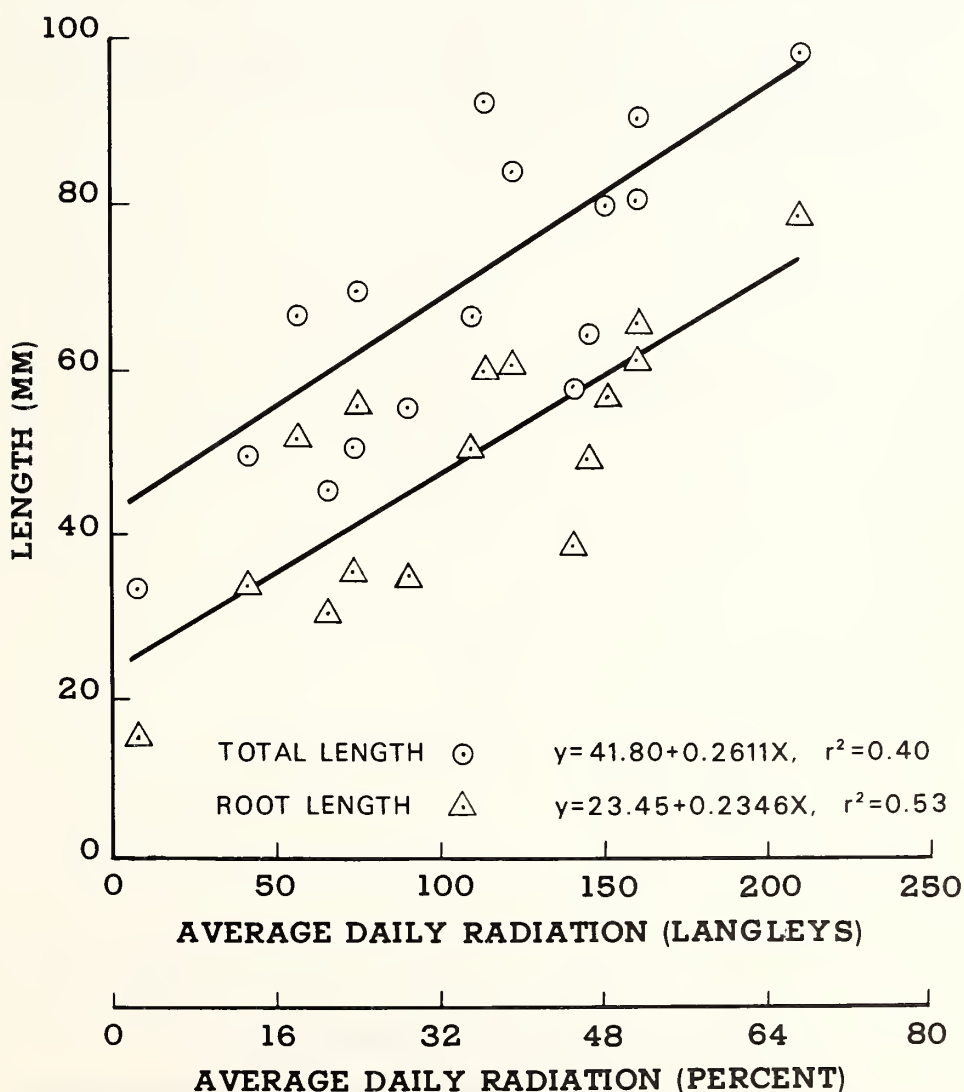
Figure 3. Increasing length of red alder with solar radiation on prepared seedspots.

await further investigation. Some seedling establishment under the shelter-wood as compared to none in the stand opening was certainly an indication that partial first-season shade was beneficial.

First-season growth showed mixed relationships with solar radiation. On the milacre plots none of the weight measurements were significant, indicating no radiation effect on dry matter production. Total length and root length averages both increased significantly with increasing averages of daily radiation while height averages did not. The main relationship with radiation appeared to be one of elongation of the root system with no increase in weight. On the other hand, seedlings growing along tractor roads showed greater height with increasing radiation, then showed decreased heights as radiation continued upward (Fig. 4). This relationship was based on a larger sample. The seedlings originated from natural seedfall, probably germinated earlier in the spring, and averaged more than twice as tall as the seedspot seedlings. The curvilinear relationship resembles that measured for western hemlock under the same conditions but contrasts with Douglas-fir heights which increased significantly with radiation with no reduction in height at the higher radiation levels (Ruth, 1967).
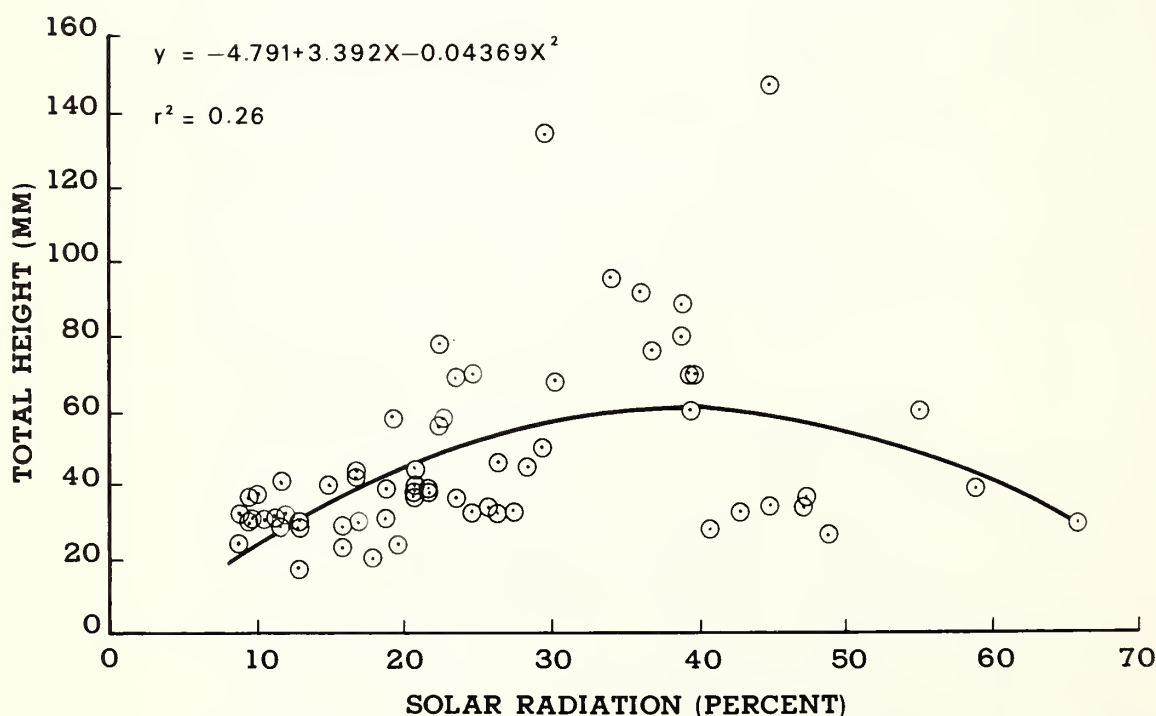
Figure 4. First season height of red alder seedlings growing along tractor roads in relation to radiation received.

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Germination analysis of grey alder (*Alnus incana*) and black alder (*Alnus glutinosa*) seeds

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Abstract

Stratification caused the germination capacity of freshly collected grey alder seed to rise from 29 to 32 percent and that of black alder seed from 28 to 35 percent. The germination potential further increased to 48 and 46 percent, respectively, as a result of a 3-day cold treatment. Under natural conditions, the establishment of grey alder reproduction was considerably better in mineral soil (33 and 36 percent) than in humus layer (3 and 15 percent). The quality classification of seed on the basis of X-ray examination corresponded to the test results obtained by various methods.

Introduction

Alders have gained increasing interest among foresters thanks to their ability to fix free nitrogen through root nodules, thereby offering certain possibilities for arranging a balanced nitrogen economy in forest soils poor in that nutrient. Such interest in alder has resulted in an active, many-sided, and rewarding research of its biology. Nevertheless, knowledge on the sexual reproduction of alder is still inadequate.

This was a study of seed germination of grey alder (*Alnus incana* (L.) Moench) and black alder (*Alnus glutinosa* (L.) Gaertn.), the two species occurring naturally in Finland, and of certain factors affecting germination. The study consisted of several questions, the most important being: How can the germination potential of seed be improved by stratification, cold treatment, and regulation of acidity of the germination medium? How can dry storage be arranged?

Experiments on these questions were carried out under carefully standardized laboratory conditions. In addition, field studies were conducted on development of grey alder between seed germination and seedling establishment, one of the most significant phases from the standpoint of reproduction.

Materials and Methods

Unsorted seeds collected from pure stands of grey and black alder were used for germination tests both in Jacobsen's apparatus and water agar as well as for experimental field sowings. The fresh seed was X-rayed and the major part of each species then dried to less than 10 percent moisture content. Part of each dried seed lot was stored at +8°C and the remainder stratified as follows:

Seeds were spread on moistened vermiculite where they could freely respire from most of their surface. The temperature of +5°C, considered best for most northern tree species (Hagner and Simak, 1958), was maintained. The stratification lasted 180 days—a period preferred within the subarctic zone, where a portion of seeds usually do not completely mature on the parent plant (Baldwin, 1942)—and it corresponded approximately to the number of days with a temperature of +5°C or less in the climatic conditions of the seed-collection site. After stratification, the seed was stored at -20°C (Tyszkiewicz, 1952) for 1, 3, 7, 14, and 30 days, respectively, to prepare it for the experiments on effects of low temperature on germination (Fig. 1).

For determining effects of acidity, a series of germination plates was prepared with pH ranging between 3 and 7 by one-unit steps. A buffer solution of sodium phosphate and citric acid was used to maintain a constant acidity in the germination medium (Table 1).
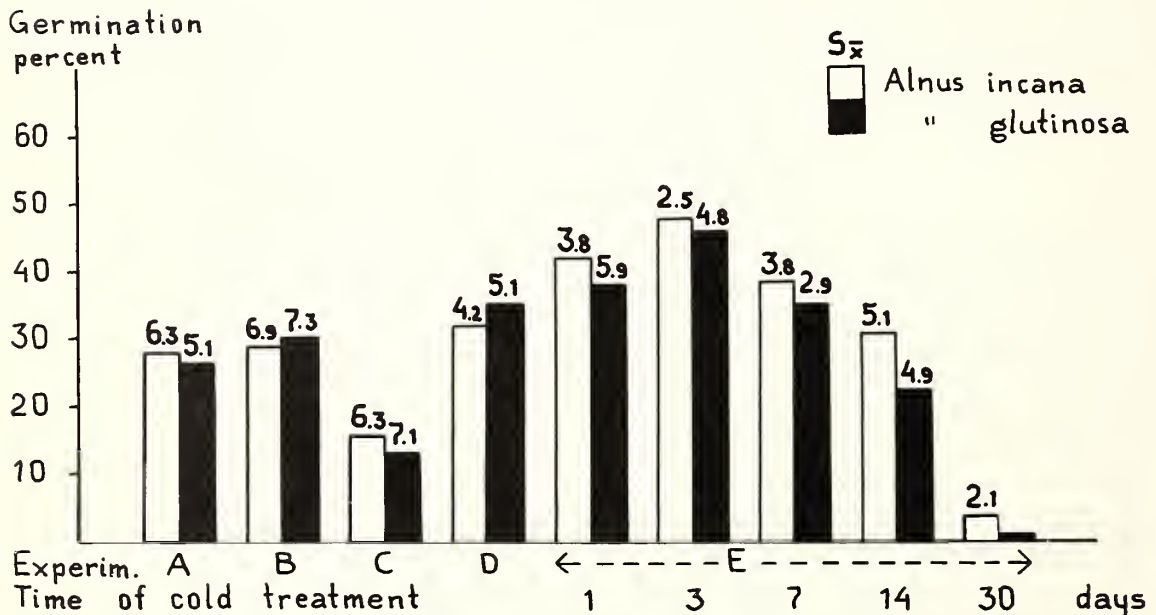
Figure 1. Results of germination experiments with *Alnus incana* and *Alnus glutinosa* seeds ("A" germinated in Jacobsen's apparatus, all the others on sterilized water agar).

A and B: freshly collected, extracted, and undried.
C: dried and stored at + 8°C for 6 months, not stratified.
D: dried and stratified.
E: dried, stratified, and cold treated.

TABLE 1. The effect of pH and cold treatment at -20°C on the germination of *Alnus incana* and *Alnus glutinosa* seed

pH	*A. incana*, cold treatment days					*A. glutinosa*, cold treatment days				
	1	3	7	14	All durations	1	3	7	14	All durations
					Germination percent, mean and $S_{\bar{x}}$					
3	29.0	36.2	31.3	24.8	28.4	28.7	24.3	12.4	10.6	19.0
	6.2	2.3	2.6	7.1		7.6	4.7	4.8	6.1	
4	36.5	44.8	34.6	23.5	32.4	41.3	50.3	38.1	17.6	36.8
	3.7	1.5	4.3	5.4		6.0	6.5	6.1	4.7	
5	44.9	52.0	41.6	31.3	42.4	26.8	38.0	32.7	17.7	28.8
	3.6	2.4	2.5	4.2		5.4	4.1	2.4	5.1	
6	30.0	33.3	26.0	21.7	27.7	20.4	12.8	10.4	8.4	13.0
	4.0	2.6	6.0	4.6		5.1	5.4	5.2	4.1	
7	18.0	20.2	17.6	11.3	16.8	3.9	3.9	0.5	0.0	2.1
	6.2	4.5	8.9	5.9		1.2	0.7			
All Levels	29.7	37.3	30.0	21.2		24.2	25.4	18.8	10.9	

The field experiments were carried out on both moist and dry forest sites. The seed was sown at the end of May on the surface of the humus layer and on scarified mineral soil.

All seed used in the experiments was surface sterilized to prevent fungal infection to which alder seed is very susceptible (Rohmeder, 1951).

The laboratory germination tests were carried out on 10 replicated lots, totaling 500 seeds per test for each species; the field experiment was on 10 replicate test lots of 100 seeds each for each species.

Results and Discussion

X-ray Photography and the Qualitative Classification of Seed

The developmental stage of the embryo and endosperm were determined by X-ray examination for qualitative classification of the seed (Simak and

Gustafsson, 1953; Simak, 1953 and 1954; Müller-Ohlsen and Simak, 1954). Three classes were devised:

0: empty
1: incompletely developed, otherwise abnormal
2: well-developed, with a complete endosperm with the embryo filling the major part of the embryonic cavity.

This qualitative classification by X-ray photography yielded the following results:

	Grey alder (Percent)	Black alder (Percent)
Class 0	45.5	43.3
Class 1	25.6	26.9
Class 2	28.9	29.8
	100.0	100.0

The distribution among quality classes was about the same for both species but considerably different from that usually found in conifers growing in similar climatic zones. In alder the best class exhibited only half the germination capacity of that of coniferous species (Hagner and Simak, 1958; Sarvas, 1962).

Analyzing seeds in classes 0 and 2 did not cause much difficulty. However, considerable difficulty was encountered with seeds falling into class 1, primarily from inability to identify the precise stage of development of embryos. Nevertheless, a common, readily identifiable phenomenon in this seed class was polyembryosis.

Unstratified and Stratified Seed

The seed germinated rapidly in most cases regardless of the type of experiment. Generally 75 percent germinated during the first 5 days and the rest during the following 3 days. No late germination occurred.

About 30 percent of the freshly collected, undried seed germinated in Jacobsen's apparatus and water agar (Figs. 1A and 1B). The germination percentage of dried, unstratified seed which had been stored for 6 months was as low as 15 percent (Fig. 1C).

The germination of normally stratified seed without cold treatment increased to 35 percent. However, after a 3-day cold treatment it reached as high as 45 percent. Prolonged cold treatment diminished germination until, after 30 days, the seed had almost entirely lost its capacity to germinate.

It is well established that stratification generally stimulates germination of tree seed. During normal stratification, gas exchange through the seedcoat is increased as a result of internal metabolic processes (Hagner and Simak, 1958). The favorable effect of short-term cold treatment on the stratification procedure is not, however, an easily explained phenomenon. The respiration of the seed in no way improves; on the contrary, it diminishes. Undoubtedly, cold treatment triggers the mechanism which regulates

enzymatic activity of the seed, as do other treatments based on use of hormones, vitamins, and acids (Holten, 1946 and 1947; Avery and Johnson, 1947; Crocker, 1948; Karlberg, 1953).

Grey alder seed endured dry storage somewhat better than that of black alder. Stratification improved the germination capacity of black alder seed more than that of grey alder. After the cold treatment which followed stratification, however, the situation was reversed. These phenomena are presumably related to the different biological-ecological nature of the two tree species.

The germination percentages of freshly collected seed of both species corresponded well to the quality class 2 determined by X-ray examination, and to the classes 1 and 2 combined for stratified seed which had received a 3-day cold treatment.

pH Effects on Seed Germination

Grey alder seed germinated best at pH 5 and black alder at pH 4. Germination was not closely restricted to these pH levels, but black alder appeared to be more sensitive to pH than grey alder, especially at pH levels higher than optimum (Table 1).

The effect of free hydrogen ions on the enzymes catalyzing germination is one possible influence of pH on seed germination (Trenel, 1925). Anions may also be important. When the anions differ from those present in this experiment, citric acid and the buffer solution of sodium phosphates, the optimum pH for germination could conceivably be otherwise. These observations do not necessarily reflect the influence of substrate acidity on germination under natural conditions. Several other factors may exert equally strong or stronger influence.

Germination on Mineral Soil and Humus in Moist and Dry Forest Sites

Germination of grey alder was considerably better on scarified mineral soil than on humus, in both moist and dry forest sites (Table 2). In mineral soil germination was even better (42.6 percent and 47.9 percent) than could be expected on the basis of X-ray examination or germination tests.

The establishment of reproduction (33.0 percent and 36.1 percent) corresponded to the germination percentage of normally stratified seed (Table 2). Favorable weather conditions during the experimental period at least in part permitted this high degree of success.

Differences between sites were particularly pronounced for the humus layer in regard to both germination (13.2 percent and 30.7 percent) and establishment of reproduction (2.9 percent and 15.2 percent). These differences likely stem from the more efficient sorption of water and more rapid and thorough drying early in the season of humus as compared to mineral soil. The reaction of the humus layer (pH 4.05 and 4.80) may also have been a factor in producing these differences.

TABLE 2. Germination 14 days after sowing, and total establishment of green alder reproduction at the end of the first growing season (5th September) on forest soil

Site and forest type	Seed spot				Germination percent, mean and $S_{\bar{x}}$		Seedlings in percent, mean and $S_{\bar{x}}$ of number of total seed sown	
	Mineral soil		Forest floor					
	Tex-ture	pH	Depth, mm	pH	Mineral soil	Forest floor	Mineral soil	Forest floor
Dry forest land (VT[1])	sand	4.6	15	4.1	42.6 5.1	13.2 6.0	33.0 4.9	2.9 .9
Moist forest land (MT[2])	fine sandy soil	4.9	29	4.8	47.9 3.7	30.7 4.8	36.1 3.1	15.2 4.9

[1] Vaccinium type of Cajander.
[2] Myrtillus type of Cajander.

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Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska[1]

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Abstract

A pedological study along a transect from the terminus of Casement Glacier to the terminal moraine of Bartlett Cove revealed soils whose historical sequence corresponds to the ontogeny of a podzol. Fresh deposited glacial till is immediately attacked by a number of processes—carbonates are depleted and cryopedological processes attain their maximum. As plants are established, organic matter enters the mineral soil and a surficial A1 horizon is formed. Soil pH decreases and cation exchange capacity increases. The addition of more plants results first in a thin litter layer (01 horizon) and then in a humified layer (02 horizon). After about 55 years, an incipient B horizon has appeared. The pH continues to decrease and exchangeable acidity to increase until exchangeable bases are considerably depleted. One hundred fifty years after deglaciation, the A2 horizon first appears. Forest floor thickness increases from 2 at 12 years to 20 centimeters after 150 years. The C/N ratio has also increased.

Existing Podzols found at the end of the recessional sequence are shallow and lack both illuvial humus and clay horizons. Since an illuvial iron horizon is present, these soils have been included among Kubiena's iron podzols.

Introduction

Time as a factor in soil formation may be evaluated following the functional, factorial approach as suggested by Jenny (1941, 1946, 1958).

If soil formation is qualitatively expressed as a function of time, we speak of a chronosequence. If it is instead expressed quantitatively, we speak of a chronofunction (Jenny, 1958).

To determine the effect of time, natural systems can be chosen where the age of the land surface is known or where chronological sequences of definite time intervals can be established. Furthermore, to determine time as a single variable, the other soil-forming factors (climate, organisms, parent material, and relief) must be kept relatively constant. Muir Inlet in Glacier

Bay National Monument, southeastern Alaska (Fig. 1), offers a unique situation for studies of soil development as functions of time. The positions of ice fronts of Muir and other glaciers have been accurately recorded since 1892. Details of glacial recession and geology for Muir Inlet have been provided by Field (1947), Lawrence (1958), Goldthwait (1963, 1966), Price (1964), and Haselton (1966). Succession of plant communities have been discussed by Cooper (1923, 1930, 1931, 1939), Lawrence (1951, 1958), and Decker (1966). Soil development has been studied by Crocker and Major (1955) and Ugolini (1966). Mammal, bird, fish, and insect populations were studied by Good (1966), Trautman (1966), Merrell (1966), DeLong (1966), and Welch (1965).

The author visited the Muir Inlet area in 1965 as a member of an ecological party organized by the Institute of Polar Studies, Ohio State University.

The Area

Muir Inlet region is situated in the northeast corner of Glacier Bay National Monument in southeastern Alaska (latitude 58°45' to 59°01' N and longitude 135°55' to 136°15' W) about 120 km (74.5 miles) west of Juneau (Fig. 1). Numerous glaciers flow in this area; all are retreating. Field (1947) estimated that in 66 years 35 percent of the area originally covered by ice (175 square km or 108 square miles) was exposed. The major study area was
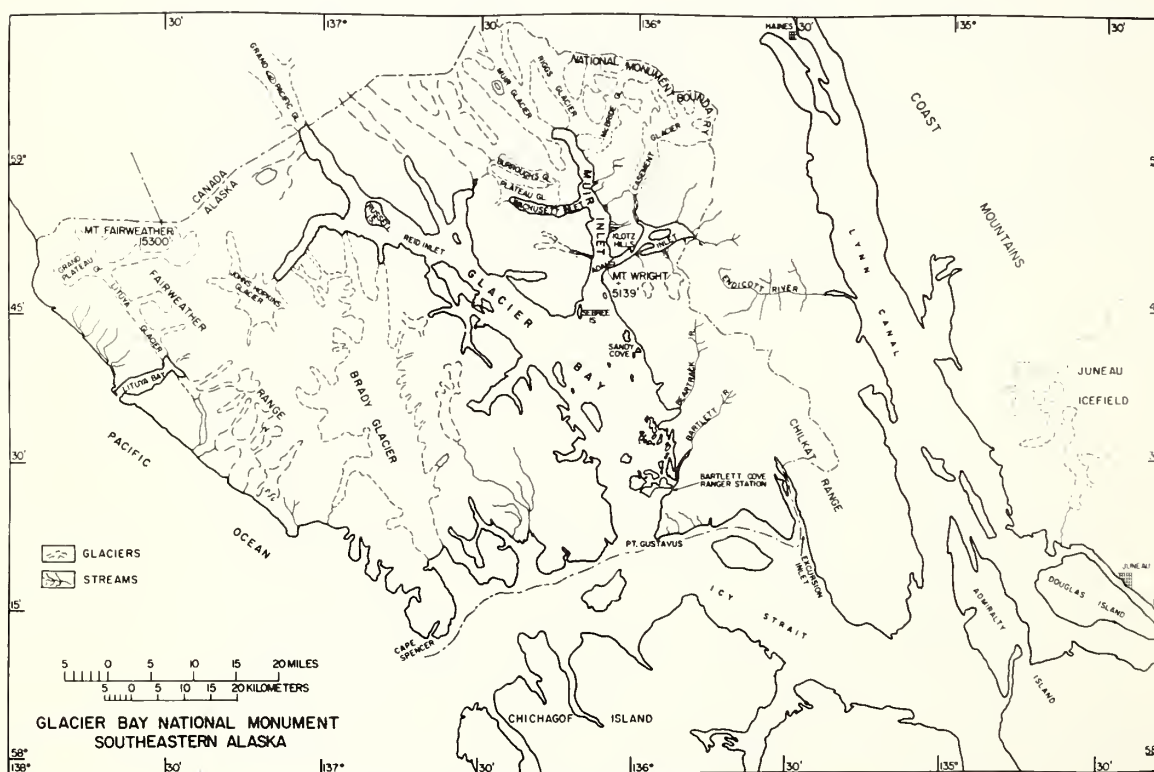
Figure 1. Glacier Bay National Monument, southeastern Alaska.

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in the 15 square km (9.3 square mile) area exposed by the retreat of Casement Glacier (Fig. 2).

Climate

The climate of Glacier Bay and Muir Inlet is predominantly maritime with small annual and diurnal temperature fluctuations, high relative humidity, persistent cloudiness, heavy precipitation, and strong winds. Crocker and Major (1955) briefly summarized the climate of the region; Loewe's (1966) discussion is more detailed and the following information is extracted from it. Persistent cloudiness reduces the duration of sunshine. Juneau data indicate May is the clearest month with a mean duration of 225 hours of sunshine for the period of 1958-64. Hours of sunshine decrease to 35 hours in December. Data from meteorological stations at Cape Spencer, Gustavus, and Haines show a progressive lowering of temperatures moving inland from the other coast. At Gustavus, near the mouth of Glacier Bay, the mean annual temperature has been 5°C (41°F) over a 29-year period and the mean annual precipitation, 1,376 mm (54.17 inches).

Weather observations were made at Muir Inlet during the summers of 1963 through 1965. Total radiation measurements made near Casement Glacier in 1965 (Terminus Station, Fig. 2) indicated that 700-750 calories per square centimeter are received on a cloudless July day. This drops to 550 calories by mid-August. Total radiation is only 100 calories on overcast days in July and 65 calories in August. Temperatures at Terminus Station and near the shore of the inlet (Delta Station, Fig. 2) were virtually the same. The mean maximum and minimum from June 18 to July 31 were 4.5°C (40.1°F) and 4.0°C (39.2°F), respectively.

Rainfall was 170 mm (7.0 inches) at Delta Station (between June 15 and July 31, 1965). Winds during this time were NE by E, weak in the morning (4.5 knots) and stronger in the afternoon (6 knots). Loewe (1966) concluded from the summer observations that no major climatic differences existed along Muir Inlet and that biological differences probably resulted from factors other than summer climate.

Parent Material

Eight formations of glacial, glacial-fluvial, and glacial-marine deposits constitute the stratigraphy of Muir Inlet (Haselton, 1965; Goldthwait, 1966). Only the upper members are important substrata on which soils and ecological successions have developed. These deposits belong to Neoglacial and Recent times. Some of the Neoglacial deposits are outwash gravel left by advancing Neoglacial ice, belonging to the upper member of the Van Horn Formation (Haselton, 1966). Where the upper till has been eroded, these gray gravels are exposed and form the parent material on which the soils developed.

The other Neoglacial deposit is the Glacier Bay till which covers much of the area. The till was laid down by the last ice advance which invaded the upper Muir Inlet about 2,735 ± 160 years B.P. and reached its maximum

Figure 2. Map of Muir Inlet, showing the positions of retreating glacier fronts by decades since 1880. Black squares indicate locations of meteorological stations.

expansion in 1700 A.D. standing near Bartlett Cove (Lawrence, 1958; Goldthwait, 1963). Since then, the ice has been retreating. Glacier Bay till mantles all other formations and is the parent material on which the soil chronofunction and 250-year-old Podzol were studied.

Recent deposits, a few hundred years old and less, consist of ablation till and glacial outwash. Ablation till forms a discontinuous layer covering the Glacier Bay till. Goldthwait (1966) estimated that 30 percent of the land surface below 300 meters exposed by retreating ice is floored by outwash gravel. Colonization by plants on the outwash gravel is not as rapid as on till because of excessive drainage. Soil development is also retarded.

The unconsolidated deposits are composed of igneous rocks (granite, granodiorite, and diorite—the latter most common), dike rocks (varying from andesite to basalt), metamorphic rocks (indurated, thin-bedded, hard, argillaceous, metasedimentary rocks that resemble chert), and limestone (light to dark gray, fossiliferous marine limestone) (Haselton, 1966).

Time

The pertinent glacial chronology concerns events following the last glacial recession. Soils discussed in this paper were developed on material left by receding Neoglacial ice that stood at Bartlett Cove between 200 or 300 years ago. The position of the receding ice front as marked on Fig. 2 was compiled by Dr. R. P. Goldthwait, Ohio State University.

Organisms

Since glacial recession was initiated 200 to 300 years ago, plants and animals have rapidly invaded deglaciated areas and have produced many different ecosystems through ecological successions. Plant succession in Muir Inlet can be divided into eight intergrading stages (Decker, 1966):

Stage I, early pioneer, 0 to approximately 5 years. Largely *Dryas drummondii* Rich and *Salix* sp. with *Equisetum arvense* L. (moist sites) *Epilobium angustifolium* L. and *Epilobium latifolium* L. (sandy sites).

Stage II, mat stage, 5 to 15 years. *Dryas* mats up to 4 meters or more in diameter.

Stage III, late pioneer, 15 to 20 years. *Dryas* mat forms a uniform carpet with scattered *Alnus incana* (L.) Moench and *Populus trichocarpa* Torr. & Gray.

Stage IV, open thicket, 20 to 25 years. Clumps of alder 2 meters or more high.

Stage V, closed thicket, 25 to 30 years. Coalesced clumps of alder form an almost impenetrable barrier.

Stage VI, poplar-line, 30 to 35 years. Scattered poplar trees emerge above alder and form a distinct horizon line.

Stage VII, spruce forest, 40 or 45 to 75 or 90 years. Sitka spruce (*Picea sitchensis* (Bong.) Carr.) dominant plant, alder dying out.

Stage VIII, spruce-hemlock forest, 75 or 90 to 200 or 300 years. Spruce-

hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest appears with the successful invasion of hemlock. Forest is carpeted with a thick moss layer.

Soils

In tracing soil development from recently deglaciated barren areas of Muir Inlet to mature Sitka spruce and western hemlock stand at Bartlett Cove (Fig. 1), the writer realized that time was not the only variable. Only topography, parent material, and regional climate could be kept relatively constant. The biotic factor and time were not constant. The ingenious reasoning of Jenny (1958) to justify constancy of the biotic factor in a chronofunction cannot be totally accepted for the entire transect. He claimed that in a chronofunction, the sum of plant disseminules is the same through time, every species has the same opportunity to grow, and the biotic factor is therefore constant. The flora developed as a result of ecological successions does not represent the biotic factor and is not an independent variable.

This writer admits that there may be situations where conditions apparently approach, as far as any natural system can, the ideal model described by Jenny (1958). One of these exists in front of Casement Glacier in an area deglaciated in the last 55 years (Fig. 2). Here, a till derived from a single glacier provides fairly uniform parent material. The vegetation may be considered constant. Biotypes and species of disseminules spreading over the area are similar to the composition of the species actually growing. The soils could, therefore, satisfy the prerequisite of a chronofunction (Jenny, 1958). This chronofunction probably could be safely extended to the alder-spruce boundary line which is dated about 100 B.P., but no further.

The purpose of this paper is to illustrate changes which the disorganized

Age (years)	5	17	24	30	41	55	90	150	250
Vegetation stages	I	II	III - IV	IV - V	V - VI	VI	VII	VII - VIII	VIII
Profile no.	38	14	15	16	1	6	37	85	94
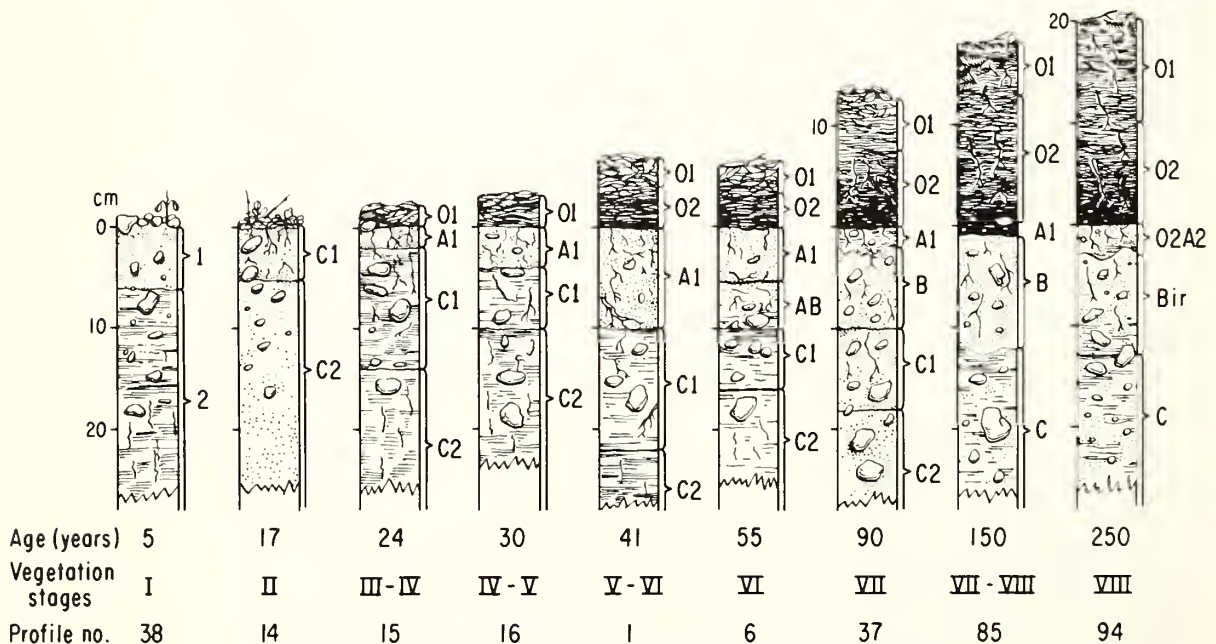
Figure 3. Soil profiles development with time, Glacier Bay, Alaska, 1965.

assemblage of glacial parent material underwent in becoming soils with definite genetic characteristics. Particular emphasis is placed on the soils colonized by alder. Much of the material is from a report previously prepared (Ugolini, 1966). Crocker and Major (1955) made a similar study in the same area but considered individual soil properties more than genesis and profile development. The morphological development of soil along the entire transect from the Casement Glacier terminus to Bartlett Cove is illustrated in Fig. 3 and 4.

Field and Laboratory Methods

Much of the study was centered in front of Casement Glacier where soils derived from a single glacial till exposed between 1965 and 1910 could be examined. Areas south of Adams Inlet, deglaciated between 1880 and 1890, and north of Beartrack Cove, deglaciated between 1830 and 1730, and the terminal moraine at Bartlett Cove, deposited between 1760 and 1660, were also investigated (Fig. 1).

Only a brief mention is made here of the procedures used in sampling, field measurements, and laboratory analyses. The reader is referred to a published report for details (Ugolini, 1966). In the field, soil blocks 15 by 15 cm were excavated to the depth of each horizon, and weight and volume of
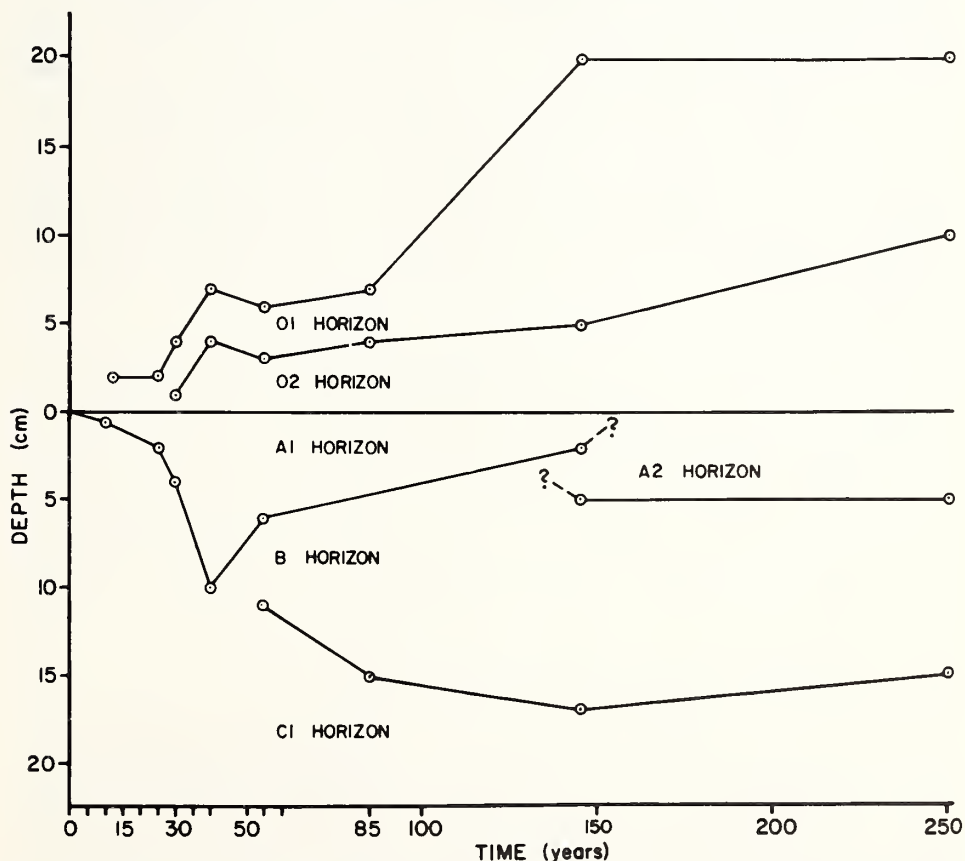
Figure 4. Graphic representation of the soil horizons development as function of time, Glacier Bay, Alaska, 1965.

included cobbles and pebbles determined. Soil moisture was determined gravimetrically. In the laboratory on the sieved samples, particle density (Blake, 1965) and mechanical analysis (Steel and Bradfield, 1934) were determined. Clacite and dolomite (Dreimanis, 1962) pH, total carbon (Peech et al., 1947), total nitrogen including nitrate (Association of Official Agricultural Chemists, 1955), exchangeable bases and exchangeable acidity (Mehlich, 1948) were evaluated. Free iron oxides were measured by Kilmer's method (1960).

Results of Field Observations

The area's maritime climate is characterized by high relative humidity, persistent cloudiness, abundant precipitation, and relatively moderate temperatures (Crocker and Major, 1955; Loewe, 1966). Consequently vegetation grows profusely, soil-leaching potentials are high, and soil development proceeds rapidly.

The first visible sign of soil formation is the appearance of an A1 horizon. Distinguished by a gray-brown color, it has a discontinuous distribution; it is found in areas deglaciated for approximately 10 years and covered by a crust of mosses and by a patchy carpet of *Dryas drummondii* (stage I). The 01 horizon (other than the living mosses) appears next and is found in areas deglaciated for about 13 years and only sparsely vegetated. After glacial retreat, it takes about 30 years to develop a thin humified layer, the 02 horizon, below dry and partially decomposed alder leaves. The area is covered mainly by alder, but willows and cottonwoods are also present (stages V and VI). Within 40 years, the A1 horizon reaches its maximum thickness then decreases until becoming indistinct after 150 years. The soils developed during the first 40 years since deglaciation are classified as Regosols.

The first appearance of an incipient B horizon is in the area deglaciated 55 years ago. This area is covered by dense thickets with interspersed black cottonwood and a few seedlings of Sitka spruce. The 'color' B horizon, only 4 cm thick, appears at the bottom of the A1 and seems to grow upward. In areas deglaciated 85 years ago are profiles where the entire A1 is replaced by a B horizon, starting directly below the 01 horizon. Other profiles still show an A1 or transition AB horizon. Dense alder thickets with interspersed spruce trees cover the area. The soils are tentatively classified as podzolic. The A2 horizon makes its appearance in areas deglaciated for about 150 years or possibly more. Its depth remains fairly constant for the next 100 years. The terrain deglaciated for about 150 years supports a mature spruce forest (stage VII). Both podzols and Brown podzolic soils are present. Bartlett Cove near the entrance of Glacier Bay (Fig. 1) was deglaciated between 200 and 300 years ago and is now covered by a mature forest of Sitka spruce and western hemlock (stage VIII). Of the 10 profiles exposed in the area, eight were podzols and two Brown podzolic. The podzols have thin A2 and Bir horizons. The Brown podzolics are similar to the ones found in the 150-year-old terrain.

In terms of the total weight of the forest floor per unit area, it appears that the accumulation of the forest floor steadily increases to a maximum for the first 150 years; thereafter, the accumulation apparently remains constant (Fig. 8). If this recessional sequence could be projected further in time, it would be possible to observe whether the 150- to 250-year stage represents the steady state or the apex for the accumulation of the forest floor. The thickness of the 01 horizon (Fig. 4) indirectly suggests that it may eventually decline. The 01 layer attains its maximum thickness in the 150-year-old surface where alder trees and other understory plants are still living and are contributing to the buildup of the floor. The 02 layer, however, appears to lag somewhat behind the 01 layer (Fig. 4), suggesting that accumulation occurs at a faster rate than decomposition. Furthermore, whereas the floor of the alder forest consists almost entirely of leaves or twigs and very few mosses, most of the floor of the mature spruce forest is made up of living and dead mosses rather than conifer needles or branches. Other characteristics of the forest floor will be discussed under the chemical properties of the soils.

Results of Analytical Determinations

The analytical data presented in this study can be calculated on three different bases: percentage weight, volume, and percentage of weight-after-ignition. Obviously, the absolute values obtained by the three methods are dissimilar; but although the trend within the profile is not always consistent, the trend along the recessional sequence is not affected. For example, the clay content in the Podzol, when calculated on the volume basis, shows an apparent accumulation in the B horizon, which would not be evident if the calculations were based on the weight.

In the following discussion, the data used for interpreting the results were obtained on the basis of the weight percentage. The data obtained on a volume basis have been used to prepare Figs. 9, 12, 13, 14, and 15. Table 1 shows the volume occupied by the different horizons as sampled in the field and the volume of the less-than-2-mm fraction including pore space in every horizon of the different profiles. These volumes were recalculated to 1 square meter of surface for preparing Tables 4 and 5.

Because mineralogical data are not available, the composition of the parent material is inferred from the pebble counts obtained in the C horizon. Furthermore, because of this limitation, the net changes in the weight of some of the components as a result of soil formation cannot be computed.

Physical Properties of the Soils

The particle size distribution of the samples shows a fair degree of uniformity (Table 2). The differences are ascribed to (a) variations in the original parent material, (b) surficial washing, and (c) frost mixing and mechanical segregation of the till soon after deposition. The Regosols, the incipient Podzolic, the Podzolic, and the Podzols are evidently too young to have developed a textural horizon. Textural differences imposed by the soil-

Figure 5. Barren terrain near the terminus of Casement Glacier. These areas were deglaciated between 1950 and 1965.

Figure 6. Area deglaciated between 1930 and 1950. In the foreground the area was deglaciated between 1940 and 1950. In the background, between 1930 and 1940.

forming processes must, therefore, be minor. Sandy textures predominate throughout, with fine silt being the next dominant fraction and clay being consistently low. Bulk density values for the entire soil and the fine earth (<2 millimeters) appear rather low; however, they are consistent within each profile and through the sequence (Table 1 and Fig. 9). The values reported by Crocker and Major (1955) for the same region are considerably higher and probably close to the actual values. These discrepancies can be attributed to the different techniques used and to the location of sampling;

Figure 7. Area north of Beartrack Cove deglaciated approximately 150 years ago.

furthermore, in this study no replicate samples were obtained; the values presented represent a single measurement for each horizon. In view of these considerations, the author hesitates to consider the bulk density values truly representative. The trend over the recessional soil sequence is similar to the one obtained by Crocker and Major (1955). A plot of the bulk density of the
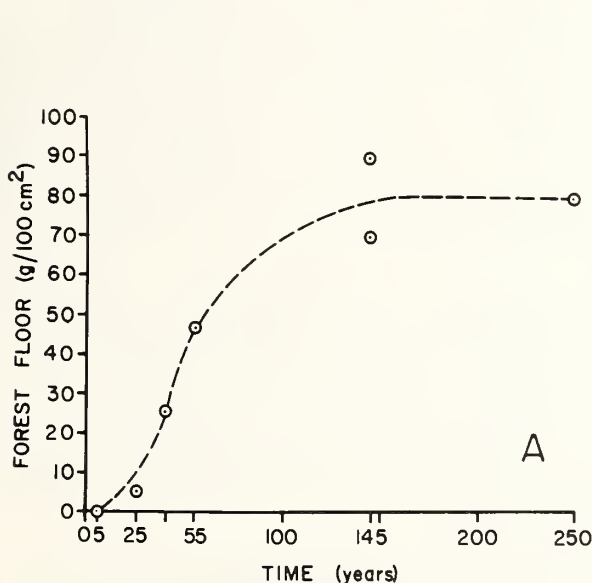
Figure 8. Accumulation of the forest floor with time. In the first 150 years under alder trees and subsequently under spruce-hemlock forest.
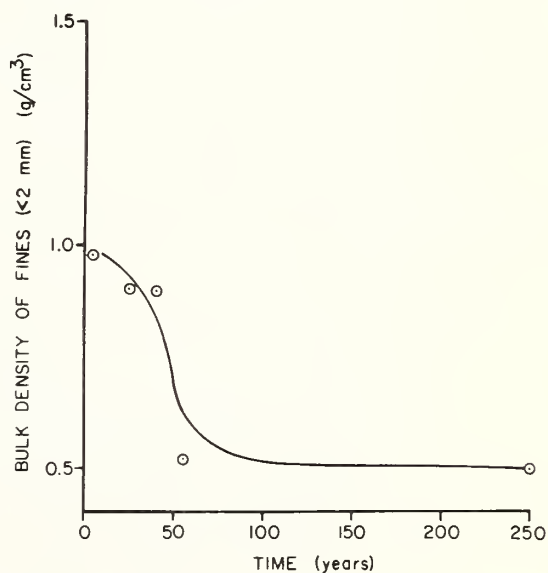
Figure 9. Bulk density of the <2mm fraction including pore space for the surficial mineral horizons.

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TABLE 1. Volumes, weights, and bulk densities of the soil horizons and <2mm fraction, Glacier Bay, Alaska, 1965

Age (years)	Horizon	Depth of sampling	Volume of[1] the horizons	Weight of[2] the horizons	Bulk density	Volume of <2mm fraction and pore space	Weight of[2] <2mm fraction	Bulk density <2mm fraction and pore space
		Cm	Cm³	Grams	G/cm³	Cm³	Grams	G/cm³
5	Profile 38:							
	1	0-6	1,350	2,018	1.49	939	929	0.99
	2	6-15	2,025	3,124	1.54	1,362	1,334	.98
	3	15-22	1,575	2,920	1.85	729	721	.99
24	Profile 15:							
	A1	0-2	450	568	1.26	340	275	.81
	C1	2-14	2,700	3,751	1.38	2,050	1,742	.98
	C2	14-18	900	1,434	1.59	580	860	.99
41	Profile 1							
	A1	0-10	2,250	3,063	1.36	1,600	1,328	.83
	C1	10-22	2,700	3,769	1.39	1,980	1,861	.94
	C2	22-32	2,250	3,381	1.50	1,496	1,391	.93
55	Profile 6:							
	A1	0-6	1,350	1,605	1.18	926	472	.51
	AB	6-11	1,125	1,431	1.27	891	801	.90
	C1	11-16	1,125	1,779	1.58	714	671	.94
	C2	16-26	2,250	3,336	1.48	1,550	1,848	.96
250	Profile 94:							
	02/A2	0-5	1,125	798	0.70	1,010	505	.50
	B	5-15	2,250	2,910	1.29	1,814	1,777	.98
	C	15-25	2,250	3,053	1.35	1,760	1,760	1.00

[1] The volume of each horizon refers to a column having a cross section of 15cm X 15cm and the depth of the horizon.
[2] Ovendry weight.

surficial horizons versus time shows that the former decreases as the age increases (Fig. 9). The decrease in bulk density with time is attributed to the incorporation of progressively large amounts of organic material in the mineral soil, development of a weak crumb structure, root channeling, and insect tunneling. The highest bulk densities among the surficial horizons are recorded in profile 38, which has formed in the recently deglaciated areas and is devoid of a surficial organic horizon.

Chemical Properties of the Soils and Forest Floor

Although no single factor can account for chemical changes, the establishment of plants and intensive leaching seem to play important roles in altering the unweathered glacial material. As Crocker and Major (1955) have shown,

TABLE 2. Mechanical analysis of samples through recessional sequence, Glacier Bay, Alaska

Age (years) and textural classes	Horizon	Depth	Sand (mm)						Silt (mm)			Clay (mm)		
			2.0-1.0	1.0-0.5	0.5-0.25	0.25-0.10	0.10-0.05	Total 2.0-0.05	0.05-0.02	0.02-0.002	Total 0.05-0.002	0.002-0.0002	<0.0002	Total 0.002-<0.0002
		Cm	- Percent -											
	Profile 17:													
Sand	1	0-6	35.0	22.0	10.8	16.3	7.3	91.4	1.4	4.2	5.6	1.4	1.6	3.0
5:	Profile 38:													
Sandy loam	1	0-6	19.8	14.2	8.0	13.1	9.7	64.8	5.4	23.5	28.9	5.2	1.1	6.3
Sandy loam	2	6-15	17.2	15.0	8.4	14.4	12.7	67.7	2.6	23.7	27.1	4.8	1.2	6.0
Sandy loam	3	15-22	15.1	14.2	8.0	13.9	11.0	62.2	9.4	22.6	32.0	4.4	1.4	5.8
24:	Profile 15:													
Sandy loam	A1	0-2	12.9	12.4	7.9	16.5	16.8	66.8	14.4	15.8	30.2	2.3	0.7	3.0
Sandy loam	C1	2-14	10.1	9.8	7.0	16.4	19.1	62.4	15.7	16.5	32.2	4.5	0.9	5.4
Sandy loam	C2	14-18	15.5	13.5	8.5	14.7	11.9	64.1	4.6	23.6	28.2	7.1	0.6	7.7
41:	Profile 1:													
Loamy sand	A1	0-10	27.3	27.2	12.8	14.6	5.6	84.6	2.5	10.6	13.1	2.2	0.8	3.0
Sandy loam	C1	10-22	13.6	14.4	9.6	15.9	10.1	63.6	1.6	27.3	28.9	6.9	0.6	7.5
Sandy loam	C2	22-33	12.1	13.4	8.9	15.2	10.4	60.0	4.8	27.9	32.7	6.3	1.0	7.3
55:	Profile 6:													
Sandy loam	A1	0-6	15.7	15.3	9.9	16.2	10.5	67.6	4.4	23.2	27.6	3.8	1.0	4.8
Sandy loam	AB	6-11	14.1	13.4	9.1	15.6	10.4	62.6	4.1	26.7	30.8	4.9	1.7	6.6
Sandy loam	C1	11-16	11.3	12.8	9.4	15.6	10.4	59.5	3.4	28.5	31.9	7.0	1.5	8.5
Sandy loam	C2	16-26	12.5	12.1	8.3	13.7	9.2	55.8	3.7	28.2	31.9	10.0	2.3	12.3
150:	Profile 85:													
Loamy sand	B	0-12	18.0	22.6	13.3	16.3	8.3	78.5	3.8	13.8	17.6	2.7	1.2	3.9
Sandy loam	C	12-55	15.7	17.4	10.8	17.5	11.0	72.4	4.5	17.4	21.9	4.7	1.0	5.7
250:	Profile 94:													
Sandy loam	02/A2	0-5	3.7	7.2	7.9	16.5	12.5	47.8	18.7	30.0	48.7	2.2	1.3	3.5
Sandy loam	Bir	5-15	10.7	14.9	11.7	18.9	10.2	66.2	8.3	21.5	29.8	3.3	0.7	4.0
Loamy sand	C	15-25	16.0	17.1	13.4	22.5	11.6	80.6	2.7	12.9	15.6	2.0	1.8	3.8

bare surfaces tend to retain a high pH even if exposed to leaching effects. They also showed that among the different plants, alder has a remarkable acidifying effect. A study by the present writer also revealed that for contemporaneous surfaces colonized by different types of vegetation, the pH values of the 0-3 layer of soil were 6.5 for alder, 6.8 for *Dryas,* and 7.0 for

mosses. The pH-time function for the entire recessional sequence for the surficial soil horizons (Fig. 10) shows the rapidity with which the reaction is dropped in the first 55 years. Iso-pH lines drawn in the deglaciated area in front of Casement Glacier illustrate the drop in pH in general and the acidifying effect of alder in particular. The alkaline pH (8.2) of the uncolonized fresh unweathered surficial till drops to 6.8 after 17 years under alder (Fig. 11). Although the acidification of the soil continues after the first 55 years, it takes between 150-200 years for the lowering of the pH by the next two units. The samples in the areas deglaciated up to 55 years ago were collected exclusively under alder trees. The sample from a 250-year-old surface was obtained under the spruce-hemlock forest.

Concomitant with the dropping of the pH, the content of carbonates decreases (Table 3, Figs. 12 and 13). As pointed out previously, the leaching becomes more effective under a vegetative cover; however, there is a distinct loss of carbonates at the surface of the soil in barren areas. An indication of the selective removal of carbonates is apparent in the ratios of calcite to dolomite (Table 3). These ratios tend to decrease as the age of the soil increases, indicating that calcite leaches more readily than dolomite. This trend holds true for all horizons, even for those that macroscopically seem to be unaffected by soil-forming processes. Evidently, the chemically unaltered material occurs considerably lower than the depth of the solum, as measured by the standard visual techniques. Werner et al. (1961) found that in Ohio the unleached material is at least 76 centimeters below the initial points of effervescence with hydrochloric acid.
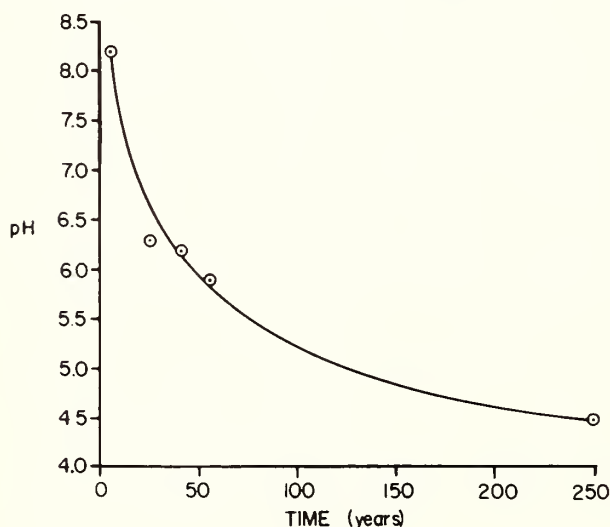
Figure 10. Changes of pH with time for the surficial mineral horizons.

Cation exchange capacity of the soil surface increases rather slowly during the 5- to 41-year period, but almost doubles between the 41- and 55-year interval and tends to increase thereafter (Table 3, Fig. 14). This trend seems to be explained if the values and distribution of the exchange capacity are related to the accumulation of organic matter in the soils. This relation seems more valid, in this case, than the one between exchange capacity and
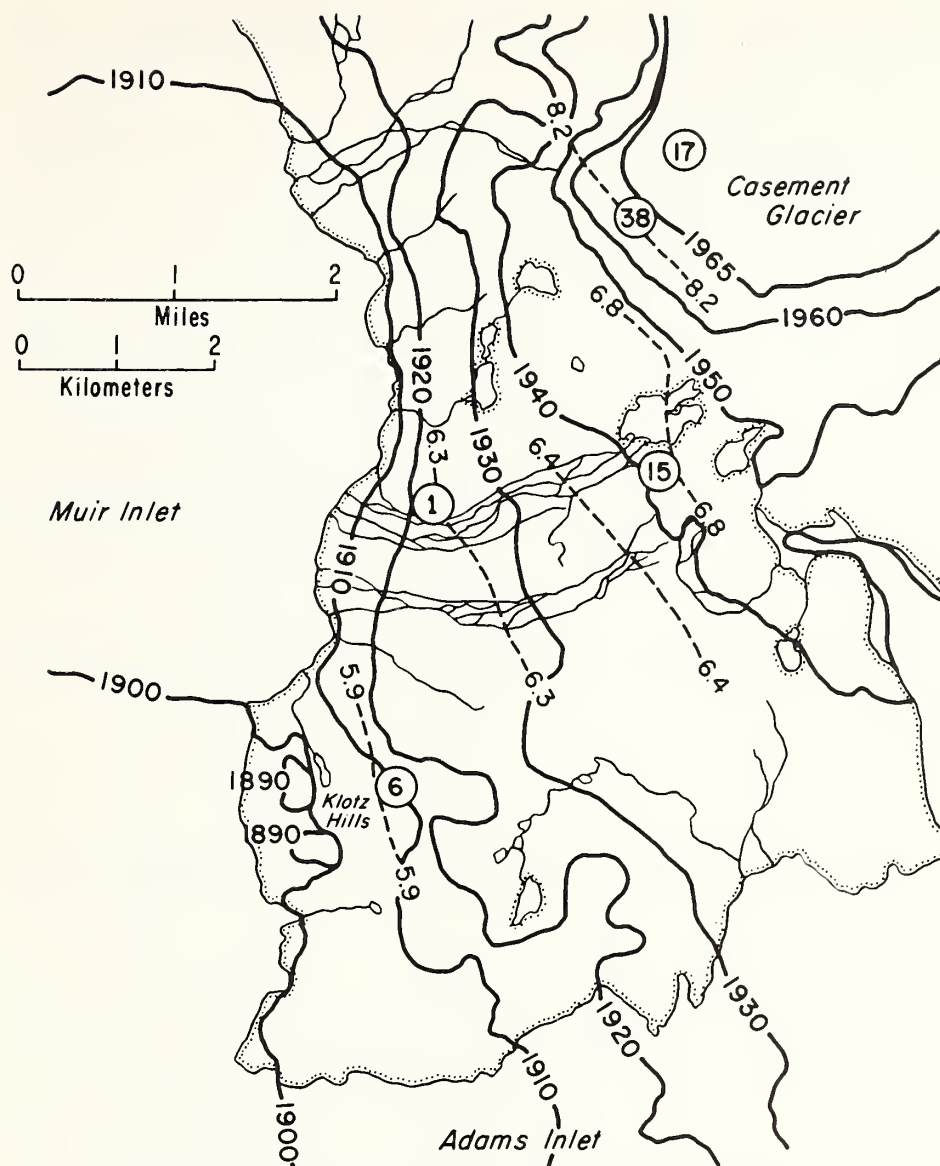
Figure 11. Iso-pH lines for the surficial mineral horizons (broken lines).

percent and distribution of clay. Because it takes about 50 years before sizable amounts of organic matter become incorporated in the upper mineral soil horizons, no substantial increase of exchange capacity is observed in the young soils. Furthermore, because the translocation of organic compounds in the profile is a slow process, only the surficial soil horizons seem to be affected by the progressive increase of cation exchange capacity with time. It probably takes 100 years before the incorporation of the organic colloids in the B horizon become significantly effective in the process of exchange. The summation of the exchangeable bases for each profile along the entire recessional soil sequence remains rather constant; only the Podzol shows a marked depletion of bases (Table 3). On the other hand, the exchangeable

TABLE 3. Chemical properties of the soils as a function of time, Glacier Bay, Alaska, 1965

Age (years)	Profile	Depth	Calcite	Dolomite	Calcite/dolomite ratio	Total carbonate	C.E.C.	H+	Na+	K+	Ca++	Free Fe2O3
		Cm	Percent	Percent		Percent	Meq/100 g		Meq/100 g			Percent
--	17	0-6	0.5	0.4		0.9	2.4	0	<0.05	2.0	1.0	0.21
5	38 1	0-6	2.1	1.2	1.7	3.4	5.0	0	<.05	1.3	4.0	.24
	2	6-15	2.8	1.1	2.5	4.1	5.0	0	<.05	1.3	4.0	.38
	3	15-22	3.4	1.4	2.4	4.9	5.0	0	.1	2.0	3.3	.33
24	15 A1	0-2	.3	.3	1.0	.6	4.0	.6	<.05	.13	2.2	.54
	C1	2-14	1.2	.9	1.3	2.2	5.0	.4	<.05	1.30	3.0	.40
	C2	14-18	2.3	1.3	1.7	3.7	5.0	0	<.05	2.00	3.2	.40
41	1 A1	0-10	.1	.4	.2	.5	6.4	1.7	.1	.70	3.0	.38
	C1	10-22	.5	.5	1.0	1.0	6.4	2.1	<.05	.70	3.0	.30
	C2	22-33	1.9	1.2	1.6	3.2	6.0	1.0	<.05	1.30	3.1	.40
55	6 A1	0-6	0	.3		.3	10.1	5.2	<.05	.13	3.8	.48
	AB	6-11	.5	.7	.7	1.2	4.4	.6	.1	.70	3.0	.44
	C1	11-16	1.2	.8	1.5	2.1	4.0	.2	<.05	1.20	3.0	.45
	C2	16-26	2.4	1.3	1.8	3.8	4.0	0	<.05	1.30	3.0	.40
150	85 B	0-12	.1	.3	.3	.4	7.8	3.3	.5	.10	4.0	.54
	C	12-55	.1	.4	.2	.5	6.0	1.8	<.05	.10	5.0	.45
250	94 02/A2	0-5	.1	.3	.3	.4	16.6	13.6	<.05	.47	1.3	.50
	Bir	5-15	.2	.3	.6	.6	12.7	11.4	<.05	.17	.9	.63
	C	15-25		.3		.3	6.3	2.6	<.05	.10	2.0	.47

(Note: H+, Na+, K+, Ca++ columns are grouped under the heading "Exchangeable cations", in units of Meq/100 g.)
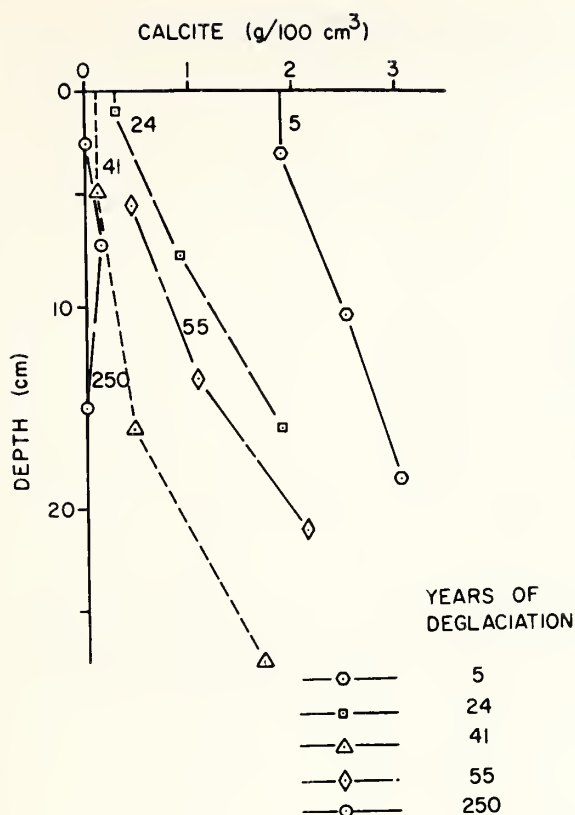
Figure 12. Distribution of calcite as function of depth for soil profiles of different ages.
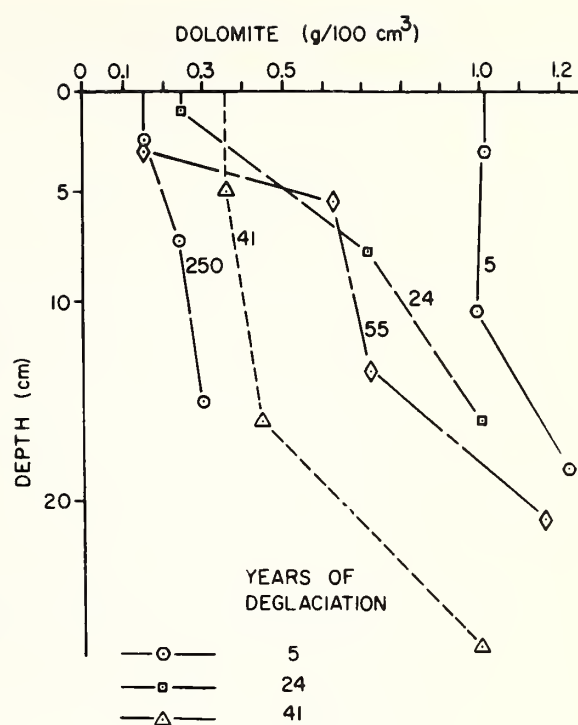
Figure 13. Distribution of dolomite as function of depth for soil profiles of different ages.

hydrogen has increased from 0.0 millequivalents in the 5-year-old soil to 13.6 in the 250-year-old Podzol (Table 3 and Fig. 14). The increase in cation exchange capacity in the sequence has been virtually taken up by an equivalent increase of exchangeable hydrogen. A corresponding situation was observed by Dickson and Crocker (1954) on Mount Shasta in California. Because cation exchange capacity is controlled by the content of organic matter and because, in turn, the exchangeable hydrogen is a function of the exchange capacity, it would appear that in this case the organic matter is the source of the acidity in the soil. The lack of appreciable depletion of calcium at the surface of the soil in the first 55 years suggests that some of the calcium is recycled from the litter zone. Magnesium was not determined, but an indication of its abundance can be obtained by subtracting the sum of the bases and hydrogen from the total cation exchange capacity. It seems that with the exception of the 250-year-old profile the rest of the soils are not well supplied with magnesium. Potassium is more abundant in the young soils and it is depleted with time. Sodium is present only as traces. The free iron oxides in the first 55 years of the soil sequence appear rather constant in the profiles (Table 3, Fig. 15). A slight increase of free iron oxides in the surface horizons could indicate a temporary chelation of the iron by the

TABLE 4. Accumulation of forest floor (01 + 02 horizons) and concentration of carbon and nitrogen in the forest floor, Glacier Bay, Alaska, 1965

Age (years)	Profile	Cover	Horizon depth	Forest floor[1]	C[1]	N[1]
			Cm	*Kg/m²*	*Kg/m²*	*Kg/m²*
5	38	None	–	–	–	–
24	15	Alder	2-0	0.52	0.26	0.011
41	1	Alder	7-0	3.78	1.54	.063
55	6	Alder	6-0	4.72	2.02	.110
150	86	Spruce	20-0	9.00	3.02	.110
250	94	Spruce	20-0	8.00	4.19	.076

[1] *Computed for the depth of the forest floor.*

organic matter or may reflect mineralogical differences in the soil material. The incipient B horizon recorded in the 55-year-old soil does not show a distinct accumulation of free iron oxides. More accumulation is evident in the B horizon in the 150-year-old soil, and definitely in the 250-year-old profile.
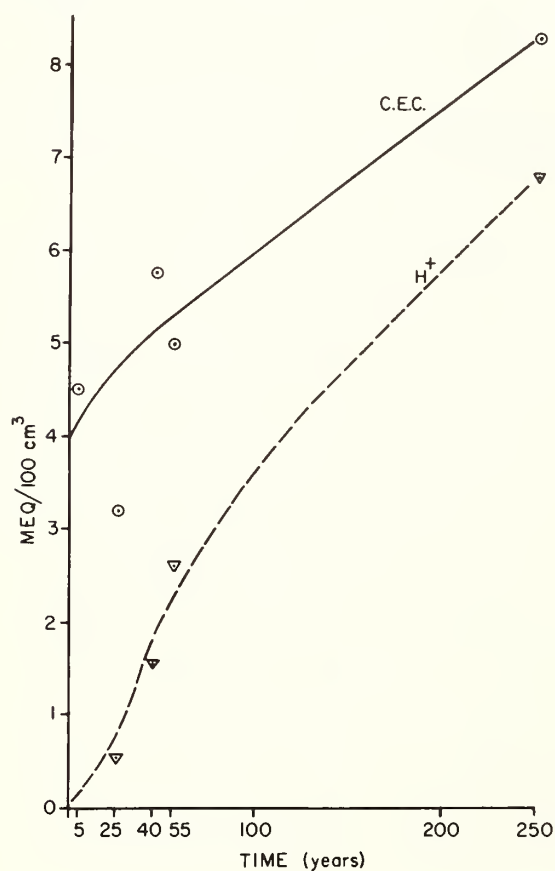
Figure 14. Changes in cation exchange capacity and exchangeable hydrogen with time for the surficial mineral horizons.

TABLE 5. Chemical properties of the soils as a function of time, Glacier Bay, Alaska, 1965

Age (years)	Profile		Depth	pH	Organic carbon	Nitrogen	C/N	L.I.[1]
			Cm		Percent	Percent	Percent	Percent
–	17	1	0-6	7.4	.12	ND[2]	--	
5	38	1	0-6	8.2	.12	ND	--	1.7
		2	6-15	8.4	.06	ND	--	1.6
		3	15-22	8.4	.06	ND	--	2.0
24	15	01	2-0	5.2	49.10	2.12	23.1	
		A1	0-2	6.3	1.00	.04	25.0	2.3
		C1	2-14	8.2	.20	ND	--	1.5
		C2	14-18	8.2	.06	ND		2.4
41	1	01	7-4	4.9	53.70	1.81	29.1	
		02	3-0	4.6	36.20	1.77	20.5	
		A1	0-10	6.2	.84	.03	28.0	2.5
		C1	10-22	7.4	.61	.02	30.5	1.9
		C2	22-33	8.0	.30	.01	30.0	2.2
55	6	01	6-3	4.4	41.50	2.33	17.8	
		02	3-0	5.1	53.70	2.54	21.1	
		A1	0-6	5.9	2.59	.09	28.8	4.0
		AB	6-11	7.4	.41	.01	41.0	1.9
		C1	11-16	8.0	.30	.02	15.0	2.0
		C2	16-26	8.1	.31	.01	31.0	2.4
150	86	01	20-15	4.0	52.20	1.09	47.8	
		02	15-0	4.4	27.55	1.00	27.6	
		B	0-12	5.9	1.04	.05	20.8	3.8
		C	12-55	7.7	.46	.02	23.0	2.2
250	96	01	20-10	4.0	56.20	.95	58.9	
		02	10-0	3.7	50.00	.06	52.1	
		02/A2	0-5	4.4	7.71	.37	20.8	13.0
		Bir	5-15	4.8	2.03	.05	40.6	5.4
		C	15-25	5.8	.64	.03	21.3	2.8

[1] L.I. = loss on ignition.
[2] ND = not detected.

The accumulation of organic carbon and nitrogen in the Glacier Bay region has been extensively discussed by Crocker and Major (1955). The present study tends to confirm in part the data obtained by these authors. For example, the total amount of litter accumulated at different times in the sequence compares closely with their values. In this investigation it was found that, starting with a barren surface, after 24 years 5,200 kg/ha of forest floor had accumulated at the soil surface. After 55 years, it had increased to 47,200 kg/ha and reached a value of 80,000 kg/ha after 250 years (Table 4). There is a progressive increase of organic carbon in both the forest litter and the soil with increasing time (Tables 4, 5, 6; and Fig. 16). Judging from the forest floor distribution, one might suspect that the organic carbon in the litter reaches its maximum probably 100 years before the soil maximum. This point cannot be proven because, of the two profiles of the 150-year-old terrain, only one, the lowest in organic matter, was analyzed. However, if this is so, the increase of carbon in the solum, after 150 years, is only due to a redistribution of carbon from the forest floor to the soil and not to a net increase in the entire profile. The annual rate of accumulation of organic carbon in the solum over the first 55 years is 12.5 g/m^2. The absence of a second organic carbon maximum in the profile of the Podzol seems to indicate that the B horizon is a color B and that it takes more than 250 years to develop an illuvial humus horizon. However, due to the inability in the field of separating part of the 02 from the A2 horizon,
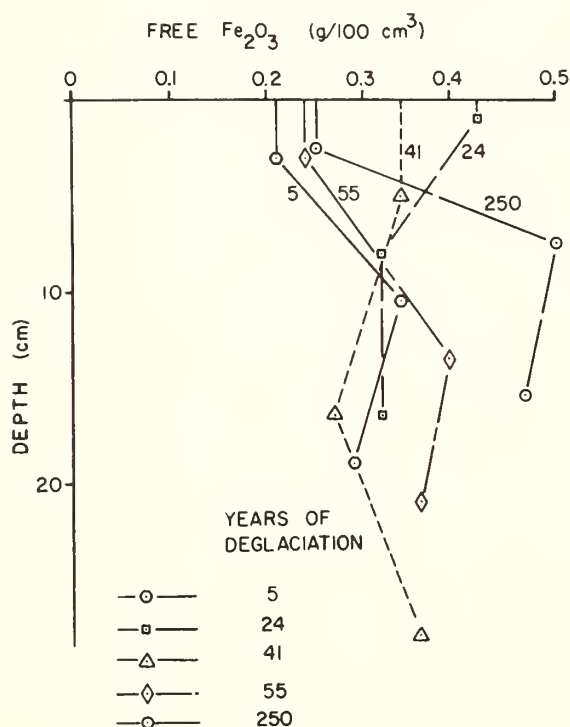
Figure 15. Distribution of free iron oxides as function of depth for soil profiles.
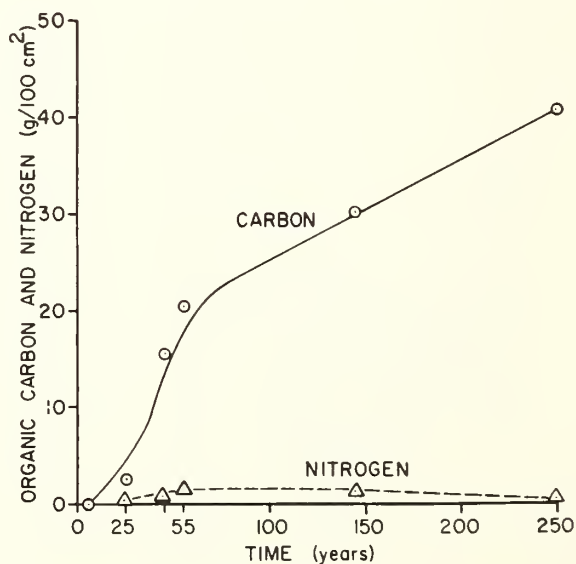
Figure 16. Carbon and nitrogen accumulation in the forest floor as function of time.

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TABLE 6. Accumulation of organic carbon and nitrogen in the soils of the chrono-function and a 250-year-old Podzol, Glacier Bay, Alaska, 1965

Age (years)	Profile	Horizons present	Solum depth	Carbon in the solum[1]	Nitrogen in the solum[1]	Carbon in the profile to a depth of 25cm	Nitrogen in the profile to a depth of 25cm
			Cm	Kg/m²	Kg/m²	Kg/m²	Kg/m²
5	38	no solum		–	–	0.086	–
24	15	A1	0-2	0.122	0.004	.339	0.004
41	1	A1	0-10	.495	.017	1.055	.035
55	6	A1 AB	0-11	.688	.022	1.006	.035
250	94	02/A2 B	0-15	3.333	.121	3.833	.145

[1] Computed for the depth of the solum.

the values reported for the A2 may be high and thus masking a possible secondary carbon accumulation in the B horizon.

Nitrogen content in the forest floor expressed on an area basis attains a plateau between 55 and 150 years and then declines (Table 5, Fig. 16). This decline occurs before 150 years; the forest floor of the 150-year-old terrain appears to be as rich in nitrogen as the forest floor of the 55-year-old forest because its volume is triple and its weight is double (Tables 4 and 5). However, when nitrogen content is estimated on the basis of weight percentage, then the maximum concentration of this element is in the 55-year-old mature alder forest (Table 5). The decreased level of nitrogen in the forest floor of the 150-year-old forest is the result of the replacement of alder by spruce. Alder can fix atmospheric nitrogen as shown by Bond (1955), Virtanen (1957), Virtanen et al. (1955) and others, whereas spruce cannot. Much of the nitrogen seems to be confined to the forest floor, and its migration in the mineral soil lags behind. Consequently, when the mineral soil acquires its maximum nitrogen content, the nitrogen in the forest floor has already declined (Tables 4, 5, and 6). The depletion of nitrogen in the forest floor with time is indicated by the increasing values of the carbon:nitrogen ratio (Table 5, Fig. 16). The increase of the carbon:nitrogen ratio in the litter zones with time reflects the replacement of the nitrogen rich alder with nitrogen poor spruce. The soils along the entire sequence showed an increase of nitrogen content with time (Tables 5 and 6). These findings are not in line with those reported by Crocker and Major (1955). They showed that approximately 120 years after deglaciation there is a depletion in nitrogen in the upper part of the mineral profile. This depletion becomes more marked after 180 years and it is ascribed to the development of the spruce forest.

This writer recognized that the failure of detecting a pattern similar to that of Crocker and Major is due to lack of analyses for profiles between 55 and 100 years and to the inability of separating the 02 from the A2 in the 250-year-old Podzol. The trend detected by Crocker and Major in the soil was verified by this writer in the forest floor.

The few discrepancies existing between this study and the one conducted by Crocker and Major should not be viewed as contradictions, due to the differing approaches to the investigation. The present study was oriented on horizon differentiations and profile development along the entire transect in general and in particular on soil parameter measurements and morphological changes during the early stages of soil formation.

Discussion

A sequence of ecosystems has developed in the Glacier Bay area along with the deglaciation stages that were initiated at the end of the Neoglaciation. Although time is the independent variable common to all the deglaciated areas, there is another variable, the biota, which is not constant throughout the recessional sequence (Cooper, 1931; Lawrence, 1958; Decker, 1966). Therefore, soil formation and development is not solely a function of time. The absence of Podzols in the alder forest, contrasting with the presence of Podzols in the conifer forest, would tend to indicate that there is a mutual relationship between the simultaneous appearance of Podzols and conifers. If so, then soil development and the biotic complex would be mutually interdependent nd time would not be the only independent variable. Thus, it was recognized that there is a stage in the recessional sequence where the biotype is constant, time is the only variable, and soil development approaches a chronofunction. The pedological significance of this chronofunction is that it coincides with the ontogeny of a Podzol. In the plant succession, the same chronofunction ends with the replacement of the alder with the spruce-hemlock forest. In a study of this chronofunction one can establish the stages, as expressed by the physical and chemical changes of the soils, through which a steady state may be reached. This is equivalent to telescoping the ontogenetic cycle of soil in equilibrium with the climate and the biota of the region.

Pedological processes seem to be accelerated in the presence of plants and more specifically in the presence of alder. Glacial deposits colonized by alder are effectively depleted of carbonates, progressively acidified, and enriched in nitrogen. After about 40 years, the alder has formed closed thickets and enough organic matter has accumulated to form a humified layer, the 02 horizon. Cation exchange capacity has doubled, and the exchangeable acidity has increased fivefold. The pH of the mineral soil has dropped two units and a pH-exchangeable hydrogen relation becomes apparent. An incipient B horizon appears in the lower part of the A1 horizon by 55 years. The forest floor acquires the highest content of N per unit weight under a 55-year-old mature alder forest. With the replacement of alder by spruce, there is a substantial decrease in nitrogen in the forest floor and the C/N ratio acquires a wider range.

In the next stage, from 55 to 250 years, the pH of the litter and of the soil has dropped still further from 4.7 to 3.8 in the soil and from 5.9 to 4.4 in the litter. The exchangeable hydrogen ion and the exchange capacity are further increased. The exchangeable bases appear considerably depleted, the carbonates are almost completely exhausted, and there is an accumulation of free iron oxides in the B horizon. The bulk density of the fines (<2 millimeters) has dropped further, and there is an increase of organic matter penetration into the soil. The A2 horizon makes its first appearance about 150 years after deglaciation. In the first 60 years, the depth of the solum as measured at the bottom of the A1 and B horizons increases from 0.5 to 11.0 centimeters, but it then increases to 15.0 centimeters during the next 190 years. This observation emphasizes that soil formation proceeds downward more rapidly during the initial stage, but as time progresses, the process of soil development involves rather the amplification of morphological, biological, physical, chemical and mineralogical properties of the single horizons.

The Podzols observed by this writer in the Glacier Bay region in the 150- and 250-year-old terrain have a shallow, bleached A2 horizon, a colored B horizon, and an accumulation of iron in the same horizon which may support the contention that these soils have not as yet approached full maturity. The suggestion by Kubota and Whittig (1960) that similar soils be classified as nanopodzols as defined by Kubiena (1953) does not seem adequate for the shallow Podzols of Glacier Bay. These soils are genetically related, although far less developed, to the Cryorthods (Podzols) of the northern part of the Cook Inlet-Susitna Lowland, Alaska, reported by Rieger and DeMent (1965), and may approximate a shallow phase of the iron-podzols described by Kubiena (1953).

Whereas the Brown Podzolic soils seem to be a necessary stage in the ontogeny of Podzols, it is not known whether they can coexist indefinitely under the same climate and biota. The prevalence of Podzols on Brown Podzolic soils at Bartlett Cove seems to indicate that eventually the Brown Podzolic soils will disappear. In the absence of additional evidence the following diagrams may be suggested:

Regosols ⟶ Podzolic soils ⟶ Brown Podzolic soils ⟶ Podzols

Regosols ⟶ Podzolic soils ⟶ Brown Podzolic soils ⟶ Podzols

⟶ Brown Podzolic soils

Regosols	Podzolic soils	Brown Podzolic soils	Podzols
0	15 years	80-100 years	approx. 150 years	250 years

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Nitrogen transformations in soils beneath red alder and conifers

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Abstract

Transformations of nitrogen in organic matter in the soil are essential to plant nutrition because nitrogen in the form of proteins and other organic compounds is not directly available. These compounds must undergo microbial decomposition to liberate nitrogen as ammonium (NH^+_4) and nitrate (NO^-_3), which can then be absorbed by plant roots.

Nitrogen transformations, particularly nitrification, are rapid in soils under coastal Oregon stands of red alder (Alnus rubra Bong.); conifers — Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), western hemlock (Tsuga heterophylla (Raf.) Sarg.), and Sitka spruce (Picea sitchensis (Bong.) Carr.); and mixed stands of alder and conifers. Nitrification is especially rapid in the F layer beneath alder stands despite a very low pH. These findings are from a study of contributions to the nitrogen economy by red alder conducted at Cascade Head Experimental Forest near Otis, Oregon (Chen, 1965).[1]

Procedures

Ammonifying capacity of the different samples was compared by testing duplicate 50-g portions, ovendry basis, of each with peptone equivalent to 1,000 ppm nitrogen. These samples, and samples of untreated soil, were incubated for 35 days at 28 C. Moisture was adjusted to 50 percent of the water-holding capacity. At the close of incubation, each sample was analyzed for NH^+_4, NO^-_2, and NO^-_3 nitrogen and for pH.

To determine nitrification rate, duplicate 50-g portions, ovendry basis, of each sample were variously treated with ammonium sulfate at 200 ppm nitrogen, with and without $CaCO_3$ to satisfy lime requirement, and without these additions. Each portion was moistened to 50 percent of water-holding capacity and incubated for 28 days at 28 C. They were then analyzed for NO^-_2, NO^-_3, and pH.

Ammonium nitrogen was determined by distilling 10.00 g samples of soil, ovendry basis, with phosphate buffer at pH 7.4 (Nichols and Foote, 1931). One hundred ml of distillate were collected in 30 ml saturated boric acid solution and titrated with N/14 sulfuric acid, using methyl red-bromcresol green indicator. Nitrite was determined on 1:5 aqueous extracts of soil clari-

[1] *This investigation was supported in part by the National Science Foundation, Grant No. GB-3214.*

fied with cupric acetate and calcium hydroxide (Harper, 1924), by a modified Ilosvay method (American Public Health Association, 1955), using 1-naphthylamine, sulfanilic acid, and sodium acetate buffer. The phenoldisulfonic acid procedure was used to determine NO_3^- in another portion of the extract (Harper, 1924).

A glass electrode was used to measure pH of 1:5 aqueous suspensions of soil; readings were made while the suspensions were stirred. Dunn's titration procedure using calcium hydroxide (Dunn, 1943) was employed to determine lime requirement.

Kjeldahl nitrogen was determined by a modified AOAC method (Association of Official Agricultural Chemists, 1960); Hibbard's mixture and a selenized granule were used in the digestion. Total carbon analyses were made on 100-mesh air-dry samples, following the high temperature combustion procedure of Allison, Bollen, and Moodie (1965). Cation exchange capacity and exchangeable cations were determined by the ammonium acetate method (Schollenberger and Simon, 1945).

All results are expressed on the basis of ovendry soil.

Results

Although samples were collected and tested at seasonal intervals, the reader's attention is directed to results of March sampling in which analyses included cation exchange capacity and exchangeable cations of the samples (Table 1). Table 2 shows the variation in different forms of nitrogen with season. Nitrite nitrogen was always less than 2 ppm, so these values are not reported.

The F layer and A11 horizon beneath alder contained significantly greater amounts of NO_3^- and Kjeldahl nitrogen and had narrower C:N ratios, despite their low acidity, than similar samples from beneath conifer stands. Cation exchange capacities were similar in both sets of samples, but the alder A11 horizon is higher in exchangeable hydrogen and lower in exchangeable calcium. These findings agree closely with those of Franklin et al. (1968), and results with respect to calcium also agree with Yamaya's comparison (1968) of A horizons beneath *Alnus inokumai, Cryptomeria japonica,* and *Castanea crenata* on an Ando soil in Japan. Yamaya attributed the lower exchangeable calcium under alder to more rapid absorption of calcium by alder than by conifers or other broadleaved trees. It seems, however, that the absorbed calcium would be recycled to a large extent by decay of fallen leaves and branches. Less exchangeable calcium in the more acid soil beneath alder could be due to leaching following replacement of calcium by hydrogen ions.

Ammonification is the first step in mineralization of organic nitrogen compounds, and the process is generally rapid. Ammonification of native organic matter (Table 3) was greatest in soil from the alder A11 horizon – about twice the rate in the corresponding horizon beneath conifers. Although total nitrogen was higher in the alder F layer, the percentage of nitrogen ammonified was the same as for the conifer F layer. Differences in

TABLE 1. Analyses of F layers and A11 horizons beneath alder and conifer stands on Astoria silty clay loam soil

Stand and layer or horizon	Water-holding capacity	pH	Cation exchange capacity	Exchangeable cations					Nitrogen			
				Na^+	K^+	Mg^{++}	Ca^{++}	H^+	NH_4^+	NO_3^-	Kjel-dahl	C/N ratio
	Percent		*Ml/100 g*	···········*Ml/100 g*···········					*Ppm*	*Ppm*	*Percent*	
Alder:												
F	420	3.6	82	1.1	1.64	10.0	9.5	59.3	15	146	2.05	17
F[1]	230	4.1	70	–	–	–	–	–	55	98	1.32	15
A11	200	3.9	68	2.5	8.1	8.6	3.8	45.1	5	67	.87	16
Conifer:												
F	290	5.1	71	.9	1.44	8.2	9.8	50.8	25	28	1.02	22
A11	206	5.3	69	4.9	5.2	16.0	12.5	30.4	25	24	.77	21

[1]*Sample collected in September; all others in March.*

transformation of added peptone were minor, total ammonification being near 40 percent except in the conifer A11 horizon in which nearly one-half of the additive was accounted for as ammonium-plus-nitrate. Much of the ammonium liberated during 35 days incubation was nitrified, so this additional NO_3^- must be included in calculating the total nitrogen ammonified. Results of analyses made after only 5 days incubation, not presented here, showed that, during the first few days of incubation, ammonification was more extensive in the less acid conifer soil.

Nitrifying capacity of the soils sampled, independent of ammonification, is shown in Table 4. Nitrification of native nitrogen was generally slow. The highest nitrification, 1.4 percent, was in the alder A11 horizon samples, and the lowest, 0.3 percent, was in the F layer under alder. Nitrification was slightly greater in samples from the conifer F layer than for the conifer A11 horizon.

Over 90 percent of added ammonium sulfate was nitrified in alder F layer samples, but only 27.5 percent was nitrified in conifer F layer samples. In A11 horizons, the order was reversed, nitrification being much lower in alder soil, probably because of very low pH. Added calcium carbonate markedly increased nitrification in both alder samples but had little influence on those from beneath conifer stands. Moreover, much of the native nitrogen in the alder F layer was nitrified, as indicated by the 293.5 percent obtained when added $CaCO_3$ increased pH from 3.5 to 4.5. An increase in exchangeable calcium could also have been important.

Discussion

These results show that soil beneath alder is higher in NO_3^- and in nitrifying capacity than that under conifers. Differences in ammonifying capacity

TABLE 2. Ammonium, nitrate, and Kjeldahl nitrogen in soil under red alder, conifer, and mixed stands at different seasons

Soil	April			July			September			March			Mean		
	NH_4^+	NO_3^-	Kjel-dahl	NH_4^+	NO_3^-	Kjel-dahl	NH_4^+	NO_3^-	Kjel-dahl	NH_4^+	NO_3^-	Kjel-dahl	NH_4^+	NO_3^-	Kjel-dahl
	Ppm	Ppm	Percent	Ppm	Ppm	Percent	Ppm	Ppm	Percent	Ppm	Ppm	Percent	Ppm	Ppm	Percent
F layer															
Alder	163	271	1.76	20	129	1.29	55	98	1.32	15	146	2.05	63	161	1.61
Mixed	–	–	--	5	113	1.43	60	160	1.77	5	131	1.28	69	135	1.49
Conifer	85	79	1.06	10	20	.64	38	10	.89	25	28	1.02	40	34	.90
All horizon															
Alder	40	140	1.13	0	47	.74	25	33	.82	5	67	.86	18	72	.89
Mixed	–	–	--	10	22	.70	40	61	.82	5	61	.64	14	36	.72
Conifer	20	71	.89	0	15	.53	8	18	.70	25	24	.77	12	32	.72

TABLE 3. Ammonification in soil beneath alder and conifer stands after 35 days incubation at 28°C

Soil and treatment	pH	Kjel-dahl	NH$_4^+$	NO$_3^-$	Total	Total at 0 day	Nitrogen ammonified	
		Percent	Ppm				Ppm	Percent
Alder F layer	3.5	2.05	240	280	520	322	169	0.9
plus peptone[1]	3.8	--	563	360	923	--	403	40.3
Conifer F layer	4.3	1.02	30	308	338	244	94	.9
plus peptone	4.3	--	330	400	730	--	392	39.2
Alder All horizon	3.6	.87	58	248	306	111	195	2.2
plus peptone	4.0	--	450	288	738	--	432	43.2
Conifer All horizon	4.6	.77	10	180	190	81	109	1.4
plus peptone	4.7	--	415	268	683	--	493	49.3

[1] At 1,000 ppm N.

TABLE 4. Nitrogen in soil from alder and conifer stands after 28 days incubation at 28° C

Soil and treatment	Ph	Kjel-dahl	NH$_4^+$-N		NO$_3^-$-N			Nitrifi-cation
			0 day	28 days	0 day	28 days	Increase	
		Percent	Ppm			Ppm		Percent
Alder F layer	3.5	2.05	174	188	148	213	65	0.3
(NH$_4$)$_2$SO$_4$ [1]	3.6	--	--	320	--	400	187	93.5
(NH$_4$)$_2$SO$_4$+CaCO$_3$	4.5	--	--	25	--	800	587	293.5
Conifer F layer	4.4	1.02	2	25	242	318	76	.8
(NH$_4$)$_2$SO$_4$	4.2	--	--	50	--	373	55	27.5
(NH$_4$)$_2$SO$_4$+CaCO$_3$	5.2	--	--	15	--	386	68	34.0
Alder All horizons	3.6	.87	32	23	79	200	121	1.4
(NH$_4$)$_2$SO$_4$	3.7	--	--	158	--	221	21	10.5
(NH$_4$)$_2$SO$_4$+CaCO$_3$	5.7	--	--	25	--	363	163	81.5
Conifer All horizons	4.7	.77	2	14	79	120	41	.5
(NH$_4$)$_2$SO$_4$	4.4	--	--	35	--	260	140	70.0
(NH$_4$)$_2$SO$_4$+CaCO$_3$	5.5	--	--	13	--	276	156	78.0

[1] (NH$_4$)$_2$SO$_4$ at 200 ppm N; CaCO$_3$ according to lime requirement of A-horizons — 25 tons/acre for alder, 17 tons/acre for conifer.

between the two stands were minor, but NH^+_4 concentrations became much greater in incubated alder soils than in incubated conifer soils. These differences, indicating that the alder soil is more fertile from the standpoint of nitrogen, are attributed primarily to nitrogen fixation by the streptomycete symbiont in alder root nodules. The contribution of red alder to soil fertility is also evident from the better growth of Douglas-fir grown in association with red alder (Tarrant, 1961).

In the mixed alder-conifer stand, values at seasonal intervals for NH^+_4, NO^-_3, and total nitrogen in soil were generally higher than under conifers but lower than in the alder stand. These intermediate nitrogen values for the mixed-stand soil were found generally throughout the four sampling seasons, particularly with respect for NO^-_3 nitrogen (Table 4).

The appreciably higher NO^-_3 nitrogen levels under red alder may also be an important factor in limiting development of certain root pathogens such as *Poria weirii* which cannot utilize nitrate. On the other hand, *Streptomyces* and certain other antagonists of *P. weirii* are favored by nitrate nitrogen (Li et al., 1967).

Despite their low pH, the coastal forest soils show a high production of nitrate nitrogen. A high nitrifying capacity is indicative of a fertile soil, not because of nitrates *per se*, but because generally good fertility is conducive to good nitrification. In most agricultural soils, nitrification requires a near-neutral reaction and a plentiful supply of calcium and other nutrients to favor the nitrifying bacteria. Typically, the rate of nitrification decreases rapidly below pH 6.0 and becomes negligible below pH 5.0. Nevertheless, nitrification does occur in some strongly acid soils, including at least certain forest soils, as demonstrated by these and other data (Bollen and Wright, 1961). In such cases, strains of bacteria that have adapted to local soil conditions are undoubtedly present.

Whether nitrate or ammonium nitrogen is the more important nutrient for trees requires further investigation. In many cases, ammonium is the preferable form of nitrogen, depending on kind and stage of plant, pH, and general assortment of ions in the soil solution (Priainshnikov, 1942; Webster, 1959).

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Effect of stemflow precipitation on chemical and microbiological soil properties beneath a single alder tree[1]

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Abstract

Stemflow from a red alder tree had a substantially greater concentration of nitrogen and dissolved solids and slightly lower pH than gross rainfall. On a weight/area basis, however, the contribution of nutrient ions in stemflow was very small compared to that in gross rainfall or throughfall. No evidence was found to indicate that enriched stemflow affected chemical and microbial properties of soil at a distance of only 2 feet from the stem. Results of this study support previous demonstration of a narrow absorption area about the tree stem as the total soil area affected by stemflow.

The volume of stemflow[2] is of little importance hydrologically, being less than 1 percent of total rainfall in mature stands of Douglas-fir (*Pseudotsuga menziesii*) (Rothacher, 1963), or western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) (Patric, 1966). On the other hand, Voigt (1960a) showed that stemflow is released to the soil in a narrow band about the tree stem. On the basis of this "absorption area," Voigt estimated that the soil surface within a radius of about 1 foot from the stem of a beech (*Fagus silvatica*) tree received about 2.5 times the amount of water falling on an equal area in the open. In hardwood stands of northeastern United States, Leonard (1961) found, on the basis of Voigt's "absorption area," that stemflow amounting to seven times the depth of gross rainfall was concentrated close to the base of the tree.

Other investigations (Voigt, 1960b; Sviridova, 1960; Mina, 1965; Maruyama et al., 1965) have indicated that stemflow is substantially richer in nutrient ions, including ammonium (NH_4^+-N) and nitrate-nitrogen

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[2] *Gross rainfall is rainfall measured in the open. Throughfall is that portion of the gross rainfall which directly reaches the forest litter through spaces in the vegetative canopy and as drip from leaves. Stemflow is that portion of the gross rainfall which is caught on the canopy and reaches the litter or mineral soil by running down the stems (Helvey and Patric, 1965).*

(NO_3^--N), than gross rainfall. Some effect of chemically enriched stemflow might also be involved in findings of Zinke (1962) that the pattern of physical and chemical properties under an individual forest tree is generally developed with radial symmetry to the tree, varying with distance from the stem.

The possibility of stemflow exerting a localized influence on soil properties was of special interest to us in connection with studies of airborne pollutants, rhizosphere microflora, and nitrogen cycling. If chemicals moved by precipitation are concentrated in significant amount near the tree stem, as a synthesis of research findings on stemflow might indicate, sampling techniques and study design would be importantly affected. With these considerations in mind, and as part of a larger study of atmospheric chemistry and localized precipitation enrichment by forest stands, we undertook the study herein described. Our objective was to improve our understanding of the contribution to soil fertility by stemflow and the relationship of some chemical and microbial soil properties to distance from a single red alder *(alnus rubra)* tree.

We asked in this study:

1. Is stemflow from a red alder tree different in chemical composition from gross rainfall?
2. Is any difference between chemical composition of stemflow and that of gross rainfall ecologically significant in the case of a 40-year-old alder tree?
3. Does the pattern of variation in chemical and microbial soil properties appear to be related to stemflow effect?

What We Did

A single, relatively isolated red alder tree, 9.9 inches d.b.h. and about 40 years old, was selected for study on an experimental plot at Cascade Head Experimental Forest on the Oregon coast. Gross rainfall, which averages 90 inches/year at the study site, was sampled from June 1963 through May 1964 in an open area adjacent to the alder stand, and stemflow and throughfall were measured beneath the study tree. A polyethylene container was located midway between the tree stem and outer edge of the canopy to collect throughfall. Three polyethylene funnels, having a total area of 1 ft², were inserted through the lid of the container. Each funnel was fitted with a Pyrex glass wool filter plug and a 10-mesh copper screen to keep coarse debris out of the collector. Two ml of toluene were added to the container to inhibit microbial action. The tree was fitted with a lead trough which conducted stemflow through Tygon tubing into a polyethylene container protected against contamination in the same manner as the throughfall collector. In June 1964, 1 ft² samples of the F layer and A11 soil horizon were taken at 2,4, and 6 ft from the tree in each cardinal direction.

Stemflow and throughfall samples were filtered through Whatman No. 5 paper, then analyzed for nitrite nitrogen (NO_2^--N) by the method of the American Public Health Association (1955); NO_3^--N by the phenoldisulfonic

method (Harper, 1924); free and replaceable ammonium (NH_4^+-N) by the method of Nichols and Foote (1931); organic nitrogen by a semimicro modification of the Kjeldahl procedure; and pH by the glass electrode. Total dissolved solids (TDS) were determined by evaporating a 100-ml aliquot of water on a steam bath, drying in a desiccator, then weighing.

Microbial and chemical analyses of -2 mm samples of F layer and A11 horizon were carried out within 3 days after sampling. After air-drying, part of each sample was further ground to -0.02 mm size for Kjeldahl nitrogen determinations. All chemical analyses were made in duplicate, and microbial determinations in triplicate.

Fifty-gram, ovendry portions of -2 mm samples of the F layer and A11 horizon samples were made up to 1:5 suspensions by adding distilled water and mechanically shaking for 10 minutes. After coarse particles had settled, pH was measured with a glass electrode. The soil suspension was then treated with cupric acetate and calcium hydroxide to obtain a clear filtrate. Excess calcium hydroxide was removed with ammonium carbonate and the filtrate was analyzed for NO_2^--N using 1-naphthylamine, sulfanilic acid and sodium acetate buffer (American Public Health Association, 1955), and for NO_3^--N by the phenoldisulfonic acid method (Harper, 1924).

Ammonium nitrogen was determined by distilling 10.00-gm samples, ovendry basis, with phosphate buffer solution at pH 7.4. One hundred ml of distillate were collected in 30-ml saturated boric acid solution and titrated with N/14 sulfuric acid, using methyl red-bromcresol green mixed indicator (Nichols and Foote, 1931). Kjeldahl nitrogen was determined by a modified AOAC method (Association of Official Agricultural Chemists, 1960); Hibbard's mixture and a selenized granule were used in the digestion; and steam distillation was employed to drive the ammonia into receivers containing saturated boric acid solution. Titration was then made with N/14 H_2SO_4, using methyl red-bromcresol green as indicator.

Microbial analyses were made by pouring triplicate plates of appropriate dilutions of sieved fresh soil with peptone glucose agar acidified to pH 4.0 for molds, and with sodium albuminate agar for bacteria and *Streptomyces* (Waksman and Fred, 1922). Incubation was at 28 C. Counts were made after 3 days for molds and after 15 days for bacteria and *Streptomyces*.

All data are expressed on the basis of ovendry soil.

What We Learned

Chemical Composition of Precipitation

Total N concentration in stemflow (Table 1) was nearly 11 times greater than that in gross rainfall. Nitrite nitrogen, a very minor component of total N, was little changed by stemflow. Nitrate N concentration was increased in stemflow about 2½ times over that of gross rainfall; that of organic N was increased more than 12 times; and NH_4^+-N concentration was increased from zero in gross rainfall to 0.12 mg/liter in stemflow.

Concentrations of NO_3^--, organic-, and total N in stemflow were about twice those in throughfall. Ammonium N was increased from zero in gross rainfall to 0.08 mg/liter in throughfall, but this concentration was only

TABLE 1. Nitrogen concentration in precipitation; mean yearly values in mg/liter, Cascade Head Experimental Forest, June 1963 through May 1964

Sample	Nitrogen				
source	NO_2^-	NO_3^-	NH_4^+	Organic	Total
Gross rainfall	<0.01	0.02	0.00	0.08	0.10
Throughfall	.01	.04	.08	.48	.53
Stemflow	.01	.09	.12	.97	1.07

two-thirds that found in stemflow. Concentration of NO_2^--N was not different between stemflow and throughfall.

The effect of stemflow on N concentration in precipitation was substantial, but the effect of such enrichment on amount of N per acre was small (Table 2). As pounds per acre per year, N in throughfall was about four times greater than that in gross rainfall, but the amount of N in stemflow was negligible because of the small area (0.05 acre) affected.

Net concentration of total dissolved solids (TDS) in stemflow (Table 3) was more than four times that in gross rainfall. In throughfall, TDS concentration was twice that in gross rainfall. On a net pounds-per-acre-per-year basis, however, throughfall contained about one-third more TDS than gross rainfall, and stemflow contained less than 1 percent of the TDS load found in open-collected precipitation.

TABLE 2. Total nitrogen in 1 year's precipitation, Cascade Head Experimental Forest, June 1963 through May 1964

Sample source	Area affected	[1] Total N per ft^2	Total N
	Ft^2	*Mg*	*Lb/acre*
Gross rainfall	43,560	13.84	1.33
Throughfall outside absorption area[2]	41,480	56.17	5.13
Throughfall onto absorption area	2,080	56.17	.26
Stemflow	2,080	5.46	.03
Total			6.75

[1] *All values are net, after deduction for N in gross rainfall.*

[2] *Radius of absorption area (Voigt 1960a) = 16.4 inches (12 inches plus 4.4-inch radius of average tree).*

Absorption area (ft^2/acre) = 2,080 (5.87 ft^2/tree − 0.41 ft^2 basal area of average tree X 381 trees/acre).

TABLE 3. Total dissolved solids (TDS) in 1 year's precipitation, Cascade Head Experimental Forest, June 1963 through May 1964

Sample source	Area affected	TDS concentration	[1] TDS per ft^2	TDS per acre
	Ft^2	Mg/liter	Mg	Lbs
Gross rainfall	43,560	17	4,190	402
Throughfall outside absorption area[2]	41,480	34	5,635	515
Throughfall onto absorption area	2,080	34	5,635	26
Stemflow	2,080	72	453	2
Total				945

[1] All values are net, after deduction for TDS in gross rainfall.

[2] Radius of absorption area (Voigt 1960a) = 16.4 inches (12 inches plus 4.4-inch radius of average tree).
Absorption area (ft^2/acre) = 2,080 (5.87 ft^2/ tree–0.41 ft^2 basal area of average tree X 381 trees/acre).

"Total dissolved solids" includes a number of ions as well as some dust that fell during dry periods or was washed from the air during rainstorms. We did not determine ionic content of the various forms of precipitation other than that of nitrogenous components, but Moodie (1964) provided some measure of TDS composition when he sampled nutrient inputs in precipitation on the Washington coast about 100 miles north of our study area. There, where precipitation for 1962-65 averaged about 78 inches (in contrast to 113 inches at our study site), average TDS weight for the 4-year period was 208 lbs/acre.[3] Three forms accounted for 82 percent of this total: chlorine, 41 percent; sodium, 23 percent; and dustfall, 18 percent.

Acidity varied little between the three types of precipitation we collected. Gross rainfall and throughfall had essentially the same pH—6.1 and 6.0, respectively. Stemflow pH was slightly lower, 5.6, which is probably due to organic acids washed from the many bark crevices in the tree stem.

Chemical and Microbial Properties of Soil

No trend is evident in chemical and microbial data for F layer and All horizon samples (Table 4) that would indicate stemflow strongly influences soil even 2 ft from the tree. Nitrite-N and pH were essentially alike at all three distances sampled. Small variations in NH_4^+ and organic N do not indicate any relationship with distance from the tree. Only values for NO_3^--N, molds, and *Streptomyces* in the F layer were higher at 2 ft than at 4 or 6 ft from the tree, and these differences were small. All characteristics measured in the All horizon 2 ft from the tree were either no different or less than those measured at one or both of the other two distances sampled.

[3] Unpublished data for 1964-65 were kindly supplied by C. D. Moodie, Washington State University.

TABLE 4. Chemical and microbiological soil properties in relation to distance of sample from a red alder tree mean values; Cascade Head Experimental Forest

Distance from tree (feet)	Soil reaction	Nitrogen				Molds	Bacteria	Streptomyces
		NH_4^+	NO_2^-	NO_3^-	Organic			
	pH	Ppm	Ppm	Ppm	Percent	X 10^-3	X 10^-6	Percent of total bacteria
					F layer			
2	4.0	27	3	91	1.18	442	8	17
4	4.1	25	2	69	1.08	399	9	10
6	4.1	31	2	63	1.34	353	18	13
					All horizon			
2	4.3	20	2	43	.76	128	5	6
4	4.3	23	2	36	.73	135	5	6
6	4.3	28	2	50	.84	145	5	20

Conclusions

The first question posed in this study was: "Is stemflow from a red alder tree different in chemical composition from gross rainfall?" We believe, from this small study, that it is. Stemflow collected from a single alder had a substantially greater concentration of nitrogen and total dissolved solids and slightly lower pH than gross rainfall. This finding agrees with a number of published data although none dealt specifically with red alder.

Our second question was: "Is any difference between chemical composition of stemflow and that of gross rainfall ecologically significant in the case of a 40-year-old red alder tree?" We found that when stemflow data for nitrogen and total dissolved solids were projected to a weight/area basis, the contribution of nutrient ions was very small compared to those from gross rainfall or throughfall. Further, we do not believe the small reduction in pH of stemflow over that of gross rainfall (5.6 vs. 6.1) has any significance, even within the small absorption area (Table 4).

Our answer to the third question: "Does the pattern of variation in chemical and microbial soil properties appear to be related to stemflow effect?" is "Probably not." We found no evidence that the levels of some important chemical and microbial soil properties were associated with distance up to 6 ft from a tree stem. Results of this part of the study convince us that Voigt's (1960a) demonstration of a narrow absorption area about the tree stem is valid as an estimate of the total soil area affected by enriched stemflow.

Findings from this study have several practical applications. Rothacher (1963) and Patric (1966) have shown the volume of stemflow from western conifers to be of little hydrological significance. We would add that ions circulated in red alder stemflow are probably of little importance in substantially enriching the nutrient capital.

In future studies of the influence of red alder stands on chemical composition of precipitation, we would probably omit stemflow measurements. Stemflow is difficult to measure and is subject to various interpretations, according to the areal basis selected by the observer on which to calculate amounts. Sampling effort might better be spent in more thoroughly measuring and evaluating the much greater amounts of nutrient ions added by chemical alteration of gross rainfall in the throughfall process.

In future studies involving soil sampling in red alder stands, we would avoid taking samples from the narrow stemflow absorption area at the base of the tree. Outside this area, we would continue to rely on random sampling without concern about distance of the sample from an individual tree.

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Chemical soil properties under coastal Oregon stands of alder and conifers

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Abstract

*Chemical soil properties were compared under (1) adjacent 40-year-old red alder (*Alnus rubra*), conifer (mainly Douglas-fir (*Pseudotsuga menziesii*)), and mixed stands and (2) adjacent 30-year-old alder and conifer stands growing on the Oregon coast. Soils on all sites were Astoria-like Sols Bruns Acides developed primarily from Eocene siltstone. Organic matter, total nitrogen, and acidity were significantly greater in A horizons under alder and mixed stands. In A11 horizons of the older stands, organic content under alder averaged one-third greater than conifer (39 vs. 29 percent), nitrogen one-third greater (0.8 vs. 0.6 percent), and pH one unit lower (4.3 vs. 5.3). A horizons under conifer stands averaged three times richer in bases than those under alder stands. Similar differences, but of a much smaller magnitude, were observed in the B horizons. Observed effects of alder on acidity and base content disagree with the generally held concept of hardwoods as base conservers. These effects may indicate greater production of acid decomposition products in the organic- and nitrogen-richer alder soils.*

Red alder (*Alnus rubra*) is the most abundant hardwood in the Douglas-fir region of western Oregon and Washington. It is an aggressive pioneer on burned and logged-over lands, particularly in coastal areas. The abundance of red alder, together with its nitrogen-fixing habit, makes it a species of great interest in effective management of Pacific Northwestern forest lands.

The soil-improving properties of alder are generally well known. Studies have shown that red alder can make a significant contribution to fertility of forested sites in the Cascade Range (Tarrant, 1961; Tarrant and Miller, 1963). However, data are not available on its influence on some of the more fertile coastal soils. A preliminary study suggested red alder not only affects the nitrogen status of such soils but has a significant influence on acidity and base content as well.

Findings of the exploratory study prompted the detailed comparison, reported here, of chemical soil properties under adjacent stands of red alder and conifer. Some results were expected; e.g., an increase in nitrogen in soils influenced by alder litter and root sloughing. Others were surprising, such as the lower base content and increased acidity of soils under alder stands as compared with those under conifer.

The Study Area

The study sites are located in Cascade Head Experimental Forest just north of the Salmon River in Lincoln and Tillamook Counties, Oregon. The area lies within the "fog belt" forest zone of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*). Red alder is common on cutover land in this zone. A marine climate provides equable temperatures, much cloudiness, frequent rain, and summer fog (Madison, 1957). Normal annual precipitation is 90 to 100 inches. Mean annual temperature is approximately 50° F, but days below freezing or in excess of 80° F are infrequent.

Soil properties were compared under adjacent contrasting cover types at two locations. The first (alder-conifer plots) utilized adjacent 40-year-old red alder (1-acre plot), conifer (½-acre plot, primarily Douglas-fir), and mixed (1-acre plot, alder and conifer) stands. These plots were created between 1935 and 1937 from mixed alder-conifer regeneration which developed on agricultural land abandoned about 1925 (Berntsen, 1961).[1] They occupy gently sloping topography, generally southwest in aspect, at an elevation of 700 feet and about 4 miles from the ocean. The alder stand has an open crown canopy and a dense shrubby understory of salmonberry (*Rubus spectabilis*) and blackbead elder (*Sambucus melanocarpa*). Relatively few shrubs or herbs occur under the very dense crown canopy on the conifer plot. The mixed plot is intermediate in quantity of understory vegetation. Complete vegetational descriptions have been provided by Franklin and Pechanec (1968).

The second study site (Widow Creek), utilized adjacent 30-year-old stands of red alder and of conifer (also dominantly Douglas-fir). They are growing on a gentle south slope at an elevation of about 900 feet, 5 miles from the ocean. As at the other site, vegetation is sparse under the conifer stand but consists of a dense cover of herbs and shrubs under the alder.

The Soil

Soils in the study area have not been classified. However, they are best characterized as Astoria-like Sols Bruns Acides, developed from deeply weathered siltstone. Parent material is a tuffaceous siltstone which is included within the Nestucca formation of Eocene age. Throughout the area, there are occasional intrusions of Tertiary basalt which result in some modification of the soil profile. The basalt in these areas is relatively fresh and unweathered, and the soil parent material was obviously siltstone.

Soils on the plots are moderately fine textured and moderately well drained. Soils exhibited no consistent differences among stands and were very similar with respect to horizon sequence and morphology. Largest variations in profile characteristics are found in depth to weathered parent material (C horizon) and degree of stoniness. Depth of solum varies from 22 inches to over 60 inches. Except in localized areas of basalt, the soils tend to

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[1] *These plots are referred to as plots 1 (alder-conifer mixture unthinned), 2 (pure conifer, thinned), and 3 (pure alder, thinned) by Berntsen (1961).*

be relatively stone free. Of 21 profiles examined two had stone contents ranging up to 70 percent — conifer plot pit 3 and mixed plot pit 2. Most profiles examined would be included in the Haplumbrept great soil group, according to the new system of classification (U. S. Soil Conservation Service, 1960). However, several profiles were classified as Dystrochrepts because of their thinner or light-colored A horizons.

The 01 horizon (Aoo) is relatively thin, averaging approximately 1 inch in thickness. It is made up of freshly fallen and partially decomposed leaves, needles, and twigs. A thin 02 horizon (Ao) was occasionally observed, but always in a discontinuous pattern.

Beneath the forest floor lies an A11 horizon, 2 to 4 inches in thickness. Color of this layer is consistently very dark brown (10YR 2/2),[2] and texture is generally a silt loam. Soil structure is weak fine, weak medium, or fine granular. This soil material is very friable when moist and slightly sticky and nonplastic when wet. Roots are abundant in all A11 horizons.

The A12 horizon averages 6 inches in thickness with a range from 3 to 9 inches. Color of this layer is a very dark brown (10YR 2/3) or dark brown (10YR 3/3). Texture is most often a silt loam; however, several profiles had A12 horizons with a silty clay loam texture. Structure is weak to moderate, fine and medium subangular blocky. The soil in this horizon is generally friable when moist and slightly sticky and slightly plastic when wet. Abundant roots are well distributed throughout the entire horizon.

An A3 or B1 horizon is usually found between the A12 and B2 horizons. This layer varies from 6 to 15 inches in thickness, with an average of approximately 10 inches. Color of this layer is most often dark yellowish brown (10YR 3/4); however, at several locations the color was dark brown (10YR 3/3). Soil texture is generally silty clay loam, although loam, silt loam, and clay loam were each encountered once. Structure is subangular blocky of varying classes and grades. The most commonly encountered structure in these layers, however, was moderate fine subangular blocky. Soil consistence is most often slightly firm when moist and slightly sticky and slightly plastic when wet. Roots are common in the A3 or B1 horizon.

The B2 horizon has the most variable thickness of all the layers — ranging from 6 to 35 inches and averaging about 14 inches. Color of the B2 horizon is generally dark yellowish brown (10YR 3/4) or brown (10YR 4/3). The most common soil texture is silty clay loam, followed by clay loam. Soil structure is generally weak to moderate, medium and fine subangular blocky. B2 horizon material tends to be friable to slightly firm when moist and sticky and plastic or slightly sticky and slightly plastic when wet. Roots are common in this layer.

Most often there is a transitional B3 horizon which in turn grades into the weathered siltstone parent material that comprises the C horizon. Generally the B3 horizon possesses many of the same characteristics as the B2 and is differentiated on the basis of gradually increasing amounts of weathered siltstone. Several profiles showed evidence of a lithologic discontinuity at the

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[2]*Munsell Soil Color notation, always referring to moist soil.*

top of the B3 or C horizon. These discontinuities probably mark changes within the stratified parent material.

Methods

In May 1966, soil pits were dug to about 60 inches at three locations in each alder-conifer plot and at one central location in each of the two Widow Creek stands. Soil profiles were described according to current U. S. Soil Survey (U. S. Soil Conservation Service, 1951, 1962) practices. Two shallower pits (24 to 36 inches deep) were also dug in each stand and sketchily described to provide more sites for sampling the surface soil. Finally, thickness of highly variable A11 and A12 horizons was measured at nine additional systematically located points in each stand.

A bulk sample of each horizon was taken from each pit, air-dried, and divided into two subsamples — one for textural and the other for chemical analysis. Bulk density samples were obtained from at least one pit in each stand using two types of volumetric core samplers, and were ovendried, and weighed. Resulting data were used to convert analytical data to a pounds-per-acre basis.

Chemical analysis was done in the Oregon State University Soil Testing Laboratory by the procedures outlined by Alban and Kellogg (1959): pH — 1:1 soil-water paste and class electrode; available phosphorus — sodium bicarbonate method; cation exchange capacity — ammonium acetate technique; exchangeable potassium, calcium, magnesium, and sodium-flame photometer; organic matter — a modified Walkley-Black method; and total nitrogen — a Kjeldahl method.

Textural analysis of each horizon was carried out by a hydrometer method.

In calculation of pounds per acre of the various nutrients, values were calculated separately for each horizon and included adjustments for stone content. Resulting horizon figures were then added for each profile to obtain data for the desired 12- or 36-inch depths.

Results

Chemistry of Individual Soil Horizons

A horizons of soils under conifer and under red alder stands differ markedly in acidity, organic matter content, total nitrogen percent, C:N ratio, calcium and magnesium content, cation exchange capacity, and percent base saturation (Table 1). These differences are usually much smaller or nonexistent in B2 horizons, however.

Acidity. — Acidity of soils from alder stands is about one pH unit lower than in soils from conifer stands (Table 1). For example, A11 horizons under alder had average pH values of 4.3 and 4.4 at the two study sites in contrast with average values of 5.3 under both of the respective adjacent conifer stands. Differences are still significant in the B2 horizon, although of much smaller magnitude; pH values in the B2 horizons appear to be converging; i.e., the alder soil becoming less acid with depth, the conifer soil more acid.

TABLE 1. – Chemical properties of A11, A12, and B2 or B21 horizons in soils under 40-year-old (alder-conifer study plots) or 30-year-old (Widow Creek) stands of pure alder, pure conifer, or mixed alder-conifer[1]

Location and Stand	Horizon	Thickness[2]	pH	Organic Matter	Total Nitrogen	C/N Ratio	Phosphorus	Potassium	Sodium	Calcium	Magnesium	Sum of Bases	Cation Exchange Capacity	Base Saturation
		Inches		Percent	Percent		Ppm	---------------------------- Meq / 100 g ----------------------------						Percent
Alder-Conifer Study Plots														
Alder	A11	2.5 (1.0 - 4.0)	4.3 (4.0 - 4.5)	37.5 (24.8 - 56.3)	1.00 (0.73 - 1.19)	21 (16 - 28)	5.0 (2.0 - 8.5)	0.94 (0.72 - 1.52)	1.05 (0.83 - 1.25)	1.30 (0.4 - 2.0)	0.98 (0.2 - 1.3)	4.27 (2.40 - 5.35)	85.0 (70.0 - 102.0)	5.0 (2.6 - 6.3)
	A12	3.4 (0 - 7.0)	4.7 (4.4 - 4.9)	23.1 (18.1 - 32.9)	0.47 (0.26 - 0.59)	21 (18 - 25)	4.1 (1.5 - 8.5)	0.72 (0.47 - 1.18)	0.82 (0.68 - 0.95)	0.66 (0.2 - 1.4)	0.30 (T - 0.7)	2.50 (1.47 - 4.03)	60.3 (57.5 - 81.6)	4.2 (1.9 - 4.9)
	B2 or B21	4.9	4.9 (4.7 - 5.0)	9.7 (5.4 - 16.8)	0.28 (0.17 - 0.40)	20 (17 - 24)	0.6 (0.2 - 1.0)	0.41 (0.26 - 0.62)	0.79 (0.65 - 0.98)	0.15 (T - 0.4)	0.04 (T - 0.1)	1.39 (1.04 - 1.70)	54.3 (43.5 - 57.1)	2.6 (1.8 - 3.3)
Mixed	A11	2.39 (1.0 - 4.0)	4.6 (4.4 - 4.8)	31.8 (26.2 - 37.4)	0.79 (0.73 - 0.82)	23 (21 - 26)	4.5 (2.5 - 6.0)	0.79 (0.58 - 1.00)	0.95 (0.77 - 1.13)	0.93 (0.30 - 1.55)	0.96 (0.50 - 1.60)	3.63 (2.35 - 4.86)	72.4 (70.0 - 80.0)	5.0 (3.6 - 6.9)
	A12	4.64 (0 - 16.0)	5.0 (4.8 - 5.1)	20.4 (13.8 - 26.4)	0.50 (0.38 - 0.62)	22 (19 - 26)	2.0 (0.5 - 5.0)	0.61 (0.26 - 0.83)	0.99 (0.72 - 1.30)	0.77 (0.20 - 1.25)	0.60 (0.20 - 1.30)	2.97 (1.88 - 3.95)	61.0 (53.5 - 65.3)	4.9 (3.5 - 6.6)
	B2 or B21	4.9	4.9 (4.7 - 5.2)	5.3 (2.8 - 9.8)	0.19 (0.14 - 0.31)	15 (12 - 18)	0.7 (0.5 - 1.0)	0.44 (0.27 - 0.79)	0.75 (0.56 - 1.13)	0.34 (T - 1.30)	0.36 (T - 1.30)	1.89 (0.87 - 4.52)	40.7 (25.3 - 48.5)	4.6 (1.9 - 9.3)
Conifer	A11	1.61 (0 - 4.0)	5.3 (5.1 - 5.5)	28.9 (21.7 - 37.8)	0.60 (0.46 - 0.66)	28 (21 - 36)	4.3 (3.0 - 6.5)	0.85 (0.49 - 1.30)	1.00 (0.72 - 1.25)	3.41 (0.40 - 7.20)	2.88 (0.1 - 5.7)	8.14 (1.71 - 15.20)	66.1 (55.0 - 77.5)	12.3 (2.6 - 20.2)
	A12	4.34 (1.5 - 9.0)	5.3 (5.2 - 5.4)	21.8 (15.3 - 32.7)	0.34 (0.04 - 0.49)	28 (25 - 35)	1.6 (1.0 - 3.0)	0.93 (0.58 - 1.79)	0.93 (0.87 - 1.05)	2.78 (0.8 - 4.0)	2.74 (1.0 - 5.2)	7.38 (3.25 - 13.84)	65.1 (61.2 - 70.0)	11.3 (5.3 - 21.4)
	B2 or B21	5.2	5.2 (5.1 - 5.3)	6.5 (2.8 - 14.5)	0.19 (0.11 - 0.37)	18 (16 - 23)	0.6 (0.2 - 1.0)	0.34 (0.12 - 0.45)	0.83 (0.65 - 1.20)	0.34 (0.2 - 0.5)	0.60 (T - 0.4)	2.11 (1.20 - 2.02)	48.6 (41.5 - 52.5)	4.3 (2.2 - 4.6)
Widow Creek														
Alder	A11	3.67 (3.0 - 5.0)	4.4 (4.2 - 4.5)	24.9 (22.2 - 27.3)	0.74 (0.69 - 0.77)	20 (18 - 21)	3.3 (3.0 - 4.0)	0.55 (0.41 - 0.66)	1.04 (0.92 - 1.25)	0.83 (0.5 - 1.2)	0.63 (0.2 - 1.5)	3.05 (2.20 - 4.61)	53.3 (47.8 - 57.6)	5.7 (4.0 - 8.0)
	A12	9.67 (8.0 - 12.0)	4.9 (4.7 - 4.9)	18.4 (14.4 - 21.0)	0.54 (0.51 - 0.58)	20 (16 - 23)	2.2 (1.5 - 3.0)	0.45 (0.37 - 0.56)	0.84 (0.78 - 0.87)	0.40 (0.2 - 0.5)	0.27 (T - 0.8)	1.96 (1.63 - 2.45)	49.3 (46.7 - 53.3)	4.0 (3.1 - 5.1)
	B2 or B21	5.0	5.0 (4.9 - 5.0)	12.3 (10.6 - 13.1)	0.39 (0.34 - 0.44)	18 (17 - 19)	1.7 (1.0 - 2.5)	0.31 (0.29 - 0.33)	0.79 (0.78 - 0.80)	0.30 (T - 0.6)	0.50 (0.1 - 0.8)	1.90 (1.71 - 2.07)	37.3 (33.2 - 43.5)	5.1 (3.9 - 5.5)
Conifer	A11	3.33 (2.0 - 6.0)	5.3 (5.1 - 5.4)	23.5 (20.8 - 26.0)	0.53 (0.46 - 0.65)	26 (23 - 29)	3.7 (2.5 - 4.5)	1.07 (0.76 - 1.31)	1.09 (1.02 - 1.20)	2.77 (1.7 - 4.0)	3.50 (2.4 - 4.2)	8.43 (5.88 - 10.53)	52.6 (47.8 - 55.5)	16.0 (12.3 - 19.4)
	A12	7.83 (6.0 - 11.0)	5.2 (5.0 - 5.4)	16.2 (12.8 - 23.0)	0.46 (0.37 - 0.57)	20 (17 - 23)	2.2 (1.0 - 3.0)	0.84 (0.41 - 1.08)	0.93 (0.78 - 1.05)	1.00 (0.2 - 1.6)	1.83 (0.5 - 3.0)	4.60 (1.89 - 6.63)	46.6 (41.3 - 51.8)	9.9 (4.6 - 12.8)
	B2 or B21	5.0	5.0 (4.9 - 5.2)	7.2 (5.4 - 8.3)	0.20 (0.15 - 0.24)	21 (20 - 23)	1.0 (1.0 - 1.0)	0.31 (0.26 - 0.33)	0.72 (0.65 - 0.78)	0.30 (0.2 - 0.5)	0.70 (0.5 - 1.0)	2.03 (1.68 - 2.25)	37.0 (34.8 - 41.3)	5.5 (4.8 - 5.9)

[1] All averages except for thickness based on five values in the alder-conifer study plots or on three values in the Widow Creek stands.
[2] Average of 14 measurements in alder-conifer study plots and five in the Widow Creek stands.

In all cases, pH values for soil under the mixed stand are intermediate between pure alder and pure conifer, although tending to be closer to the alder soil. pH values recorded in this study are similar to those obtained in the same stands by Franklin[3] and by Bollen and Lu (1968).

Organic matter content. — A horizons have very high organic matter contents (Table 1), particularly in A11 horizons which in the field appear as distinctive, very dark brown horizons dominated by mineral particles. Differences in organic matter content between the A11 horizons under different stands are large at the alder-conifer study site — contents average 37.5 percent under pure alder and 28.9 percent under pure conifer. Data from lower horizons are inconsistent; organic matter contents are slightly higher in B2 horizons under alder than under conifer, but contents in the B2 horizons sampled in the mixed plot are lower than either. Also, greater differences in organic matter content occur in B2 horizons at Widow Creek than in A horizons.

Total nitrogen and C:N ratio. — Nitrogen contents of surface soils under alder consistently average higher than those under conifer — 0.4 percent on the alder-conifer plots (Table 1). Greatest differences are again found in A horizons, but differences are still distinct in B2 horizons.

On the alder-conifer study site, C:N ratios in A horizons under alder average 21 whereas those under conifer average about 28. Similar differences are encountered on A11 horizons at Widow Creek, but alder and conifer soils average the same in A12 horizons. The C:N ratios of the B2 horizons do not differ significantly.

On the mixed plot, nitrogen percent and C:N ratio of the A horizons are intermediate between the alder and conifer plots. Data from the B2 horizon of the mixed plot are not consistent in their ranking relative to the alder and conifer soils; however, total nitrogen percentage of the mixed soil is the same as that in B2 horizons of the conifer soil, whereas the C:N ratio is lower than that in the B horizon of either the conifer or alder soil.

Bollen and Lu's (1968) values for total nitrogen in a given horizon are considerably higher than ours, and conversely, their C:N ratios are generally lower. Except for the relative nitrogen contents of B horizons under alder and conifer, the stands have the same relative ranking, however.

Available phosphorus. — There are no significant differences between soils developed under different vegetative covers in amount of available phosphorus (Table 1). All profiles have greater amounts of available phosphorus in A horizons and lesser amounts in B horizons.

Exchangeable bases. — Quantities of exchangeable bases were low in all soils examined, but they were distinctly lower in soils under alder stands than in soils under conifer stands (Table 1). Base content (sum of exchangeable K^+, Na^+, Ca^{++} and Mg^{++}) of A horizons under alder was half or less of those under conifer. If anything, differences were more pronounced in A12 than in A11 horizons. Data from B2 horizons indicated the same relative

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[3]*Franklin, Jerry F. A fertility analysis of the soil under alder, alder-conifer, and conifer cover. 1962. (Office report on file at Pacific Northwest Forest & Range Exp. Sta., U. S. Forest Serv., Portland, Oregon.)*

ranking of stands, but all B horizons were so poor in bases that differences were very small.

Practically all of the difference in base content of soil is due to differing amounts of exchangeable calcium and magnesium. Exchangeable calcium is two to three times more abundant in A horizons under conifer compared with alder, and differences in exchangeable magnesium are even greater. There are no significant differences between stands in amount of exchangeable potassium and sodium.

These data on exchangeable bases agree with the data obtained by Franklin.[4] Bollen and Lu (1968) reported greater total quantities of exchangeable calcium and magnesium in all stands, but there was still three to five times as much calcium and about twice as much magnesium in the conifer soil as in the pure alder or mixed stand soils. Bollen also recorded greater amounts of exchangeable potassium, but found soil under alder and mixed stands superior to that under conifer in this nutrient.

Cation exchange capacity. – Cation exchange capacities are high and follow trends in organic matter content very closely (Table 1). Average cation exchange capacity of A horizons is greatest under alder and least under conifer, with the mixed stand intermediate. Differences are greater between alder and conifer at the alder-conifer study plots than at Widow Creek, probably reflecting the relative organic matter percentages at the two sites. Cation exchange capacities of the B horizons are lower than those of A horizons. However, except for the mixed plot (for which B horizon data on organic matter content and nitrogen percentage are also inconsistent), B horizons under alder still have higher average cation exchange capacities than those under conifer.

Base saturation. – Base saturation percentages are extremely low, around 4 to 5 percent in A horizons under alder and 10 to 16 percent under conifer. Base saturation in B2 horizons is about 4.5 to 5.5 percent except in soils under the 40-year-old alder stand. These low values reflect the high cation exchange capacities of the soils and very low quantities of exchangeable bases (Table 1).

Total extractable bases were not determined directly in this study. Base saturation percent was calculated by summing exchangeable K^+, Na^+, Ca^{++}, and Mg^{++}. Base saturation percentage was 40 to 70 percent higher when total exchangeable bases were determined directly.[5] Bollen and Lu (1968) found higher base saturation values than we did, even though they did not determine exchangeable sodium.

Total Quantities of Nutrients

When the values previously discussed are placed on a pounds-per-acre basis – adjusted for horizon thickness, stone content, and bulk density – the magnitude and importance of some differences are more apparent. Pounds per acre of total nitrogen, available phosphorus, and exchangeable potassium, calcium, and magnesium to 12- and 36-inch depths are shown in Tables

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[4] *See footnote* 3.

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[5] *See footnote* 3.

2 and 3. Data for the surface 12 inches are more meaningful since each average is based on a larger sample and because the relative influence of different cover types is more easily seen in the surface soil.

Weight of nitrogen (lbs/acre) is much greater under alder or mixed stands than in soils under conifer stands. At the alder-conifer study site, there is 65 percent more nitrogen under the alder stand than under conifer in the upper 12 inches (8,095 vs. 5,308 pounds per acre), and 70 percent more in the upper 36 inches (16,682 vs. 11,721 pounds per acre). Differences are not so great at Widow Creek, although the soil under alder is still significantly higher.

Differences in weight of available phosphorus and exchangeable potassium (lbs/acre) (Tables 2 and 3) are relatively small and inconsistent (e.g., compare relative pounds of phosphorus under alder and conifer at 12- and 36-inch depths). Typically, there are 2 to 4 pounds of phosphorus and 300 to 400 pounds of potassium per acre in the upper 12 inches of soil and 2 to 2½ times this amount to 36-inch depth. The only exception was at Widow Creek where weight of potassium was consistently less in the alder soil than in the conifer soil.

The greatest differences between soils under alder and conifer are in pounds per acre of calcium and magnesium (Tables 2 and 3). In either the upper 12 or 36 inches, there is over three times as much calcium in soils from conifer stands as in those under alder stands, and six or seven times as much magnesium. Soils from the alder and mixed plots were similar in quantity of calcium and magnesium (178 and 171 pounds per acre of calcium, 46 and 99 pounds of magnesium) relative to the amounts found in soil from the conifer plot (607 and 331 pounds per acre of calcium and magnesium, respectively).

Discussion

These data are typical for a coastal Oregon forest soil – high acidity, low base saturation, and high organic matter content. Values are generally within ranges reported by the Forest Soils Committee of the Douglas-fir Region (1957), although organic matter and total nitrogen percentages are somewhat higher. Three items require special consideration, however – the contrasting effects of alder and conifer on soil nitrogen, base content, and acidity.

The contribution alder and its nitrogen-fixing symbiont can make to the nitrogen status of soils is well known. Tarrant (1961) and Tarrant and Miller (1963) compared soil properties under adjacent stands of mixed red alder-Douglas-fir and pure Douglas-fir on an area which had been burned repeatedly in the southwestern Washington Cascade Range. Both studies showed higher levels of soil nitrogen in the 0- to 3-inch depth under the mixed stand – 0.25 vs. 0.14 percent – with significant differences extending to at least 21 inches in depth (Tarrant and Miller, 1963). Nitrogen had accumulated at an average annual rate of 36 pounds per acre more in the mixed than in the pure conifer stand. Similarly, Crocker and Major (1955) and Ugolini

TABLE 2. – Weight of various nutrients in the upper 12 inches of soil[1]
(In pounds per acre)

Location and stand	Total nitrogen		Available phosphorus		Exchangeable potassium		Exchangeable calcium		Exchangeable magnesium	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Alder-conifer plots:										
Alder	8,095	6,560 to 9,020	4.0	2.1 to 6.8	386	304 to 612	178	85 to 355	46	9 to 99
Conifer	5,310	3,810 to 6,270	2.3	1.7 to 3.0	389	142 to 650	607	163 to 1,170	331	104 to 584
Mixed	6,680	6,090 to 7,530	2.7	1.4 to 4.3	297	173 to 417	171	54 to 305	99	45 to 206
Widow Creek:										
Alder	7,370	6,920 to 7,625	3.2	2.7 to 3.8	234	201 to 267	132	63 to 191	59	7 to 162
Conifer	6,450	5,970 to 6,910	3.1	2.3 to 4.0	441	309 to 575	314	227 to 410	337	219 to 504

[1] Averages for alder-conifer plots based on five profiles per plot; those for Widow Creek based on three.

TABLE 3. – Weight of various nutrients in upper 36 inches of soil[1]

(In pounds per acre)

Location and stand	Total nitrogen		Available phosphorus		Exchangeable potassium		Exchangeable calcium		Exchangeable magnesium	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Alder-conifer plots:										
Alder	16,680	15,810 to 17,400	7.4	5.2 to 9.1	1,167	975 to 1,371	324	157 to 525	131	17 to 249
Conifer	11,720	8,210 to 14,610	8.3	4.8 to 14.9	920	515 to 1,172	1,123	476 to 1,602	508	134 to 736
Mixed	12,640	10,815 to 15,207	5.1	4.6 to 5.9	805	512 to 1,090	246	54 to 447	176	45 to 431
Widow Creek:										
Alder	15,160		6.7		668		193		252	
Conifer	14,530		7.3		1,095		564		1,048	

[1] *Averages in the alder-conifer plots are based on three profiles; there is only one value per plot at Widow Creek.*

(1966) have shown *Alnus sinuata* is responsible for a rapid buildup of soil nitrogen on recently deglaciated moraines. Ovington (1956a) found the nitrogen content of litter and mineral soil highest under an *Alnus incana* plantation out of five species present in one of his study areas.

Our study revealed that alder will fix significant quantities of nitrogen, even on sites already having high nitrogen levels. The soil under the conifer stands apparently contains about 12,000 pounds per acre of nitrogen. This nitrogen level is much higher than any previously reported for Northwest forest soils, although two or three other soils comparable or superior in nitrogen fertility have been reported from California's redwood region (Cooper, 1965).

Increased soil acidity and reduced base content in soils under alder had been suggested in an exploratory study.[6] Generally, however, hardwoods are considered to reduce soil acidity and build up soil fertility through conservation of bases and accumulation of organic matter. This relationship is due to low acidity and high base content of most hardwood leaf litters (Lutz and Chandler, 1946). For example, Daubenmire (1953) found that litter of *Populus tremuloides* was superior in average nutrient content to that of any northern Idaho conifers studied. Average calcium, potassium, and nitrogen contents of the aspen leaf litter were all higher than for the conifers. Tarrant et al. (1951) found that red alder supplied large quantities of leaf litter annually and this litter had the highest nitrogen content of 10 conifers and two hardwoods studied. Contents of calcium and phosphorus were above average for the 12 species. Litter of *Alnus rugosa* ranked first in nitrogen percent and fourth in calcium content when compared with that of three associated conifers and two other hardwoods (Voigt, 1965). Tarrant (1961) found calcium, magnesium, and potassium contents of the soil higher under a mixed stand of red alder and Douglas-fir than under a pure stand of Douglas-fir, although not significantly so.

On the other hand, soils under alder cover are often more acid or lower in bases, or both, than comparable soils under conifer stands. For example, at one site where Ovington (1958) and Ovington and Madgwick (1957) were able to compare soils under a plantation of *Alnus incana*, Douglas-fir, *Pinus nigra, Larix leptolepis* and *Betula alba*, litter and soil under alder ranked third in calcium and magnesium content. Soil acidity was greater only under Douglas-fir. On another site, soil pH was lowest under *Alnus incana* when compared with soils under plantations of eight conifers and two other hardwoods. Yamaya (1968) found soil under a stand of *Alnus inokumae* had a much higher exchange acidity, a smaller quantity of exchangeable calcium, and a much lower pH than comparable soils under *Castanea crenata* or *Cryptomeria japonica*. Yet the calcium oxide content of fresh *Alnus inokumae* litter, when compared with three other hardwoods and three conifers (including the above), was exceeded only by that of *Thujopsis dolabrata*. Crocker and Major (1955) and Ugolini (1966) have both pointed out the acidifying influence of *Alnus sinuata* on morainal soils.

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[6]*See footnote 3.*

Karpachevskiy (1963) found the Ao horizon under Kamchatka alder was not only one of the most acid, but also ranked seventh out of eight species studied in CaO content. In his article, he also compares characteristics of A1 horizons under different plant communities — acidity and exchangeable $A1^{+++}$ was highest under the alder thicket formation. Tarrant et al. (1951) compared the pH of "Ao" horizons under 12 Northwestern species and found the litter was not particularly acid — alder was 10th in a ranking from the most to the least acid. However, the surface soil beneath this Ao layer was the most acid of soil from under all 12 species. A similar phenomenon is apparent in Voigt's (1965) study — after 3 months of laboratory incubation or 15 months of greenhouse pot culture, litter of *Alnus rugosa* was the most acid of three hardwood and three conifer species studied.

Apparently, either acidity is sufficiently high or amount of exchangeable calcium is low enough under the alder stands we studied to be limiting for some biological processes. Bollen and Lu (1968) found addition of calcium carbonate greatly increased nitrification in soils under alder and mixed stands, but had no influence in the conifer soils.

What explanation can we offer for increased soil acidity and reduced base content in soils developing under alder cover? Our explanation is only conjectural until more research can be carried out, but considers the following points. First, an explanation apparently must be sought in the decomposition process and products and not in the chemical nature of fresh alder litter (with an exception noted below). Red alder litter is not particularly acid (Tarrant el al., 1951), and base content of alder litter is average or better than that of most associated forest species (Tarrant et al., 1951; Yamaya, 1968).

Second, in our study area an abundance of nitrogen-rich litter is deposited annually on the soil surface. Decomposition is rapid in the mild, wet coastal climate. Considerable acidity, i.e., carbonic acid and hydrogen ions, is a byproduct of decomposition processes and of the nitrification process, as ammonium-N is converted to nitrate-N.

These abundant acid byproducts, together with a rainfall of around 100 inches, could result in considerable leaching of already limited exchangeable bases from the surface soil under alder stands. Balci's (1964) comparison of leachates from red alder and Douglas-fir forest floors in the Puget Sound area appears to substantiate this hypothesis. He found red alder leachates had higher concentrations of nitrogen, phosphorus, potassium, calcium, magnesium, and tannin and lignin compounds than leachates from Douglas-fir forest floors. Furthermore, the magnitude of elemental leaching beyond 15-cm depth was Ca>Mg>K>N>P.

However, available data on mineral composition of forest stands suggest that at least a portion of the calcium absent from soil under the alder may be found in the standing crop of trees and understory vegetation. Hardwoods, including alder, typically contain a much greater amount of calcium than do conifers, when growing on comparable sites (Ovington, 1962). Although there is a greater cubic volume of wood in the conifer stand (Berntsen, 1961), more pounds of calcium are probably incorporated in the red alder

stand. Similarly, the calcium content of flora under a stand of *Alnus incana* was found to be much higher than that of flora under other forest stands (Ovington, 1956b). If a similar situation exists at Cascade Head, it would further increase the difference between alder and conifer stands in amount of calcium present in the biomass, particularly since the understory vegetation is much more abundant under alder (Franklin and Pechanec, 1968).

One final thought: Red alder leaf litter contains a phenolic compound not present in any associated conifers. Thus, there are possibilities that this substance, or one of its byproducts, or some other organic compound unique to this genus, effectively mobilizes bases and facilitates their removal from surface soils.

Results of this study suggest some important areas for future investigation. We now know alder will make a significant contribution to the nitrogen economy of almost any site on which it will grow. But how widespread is its effect on soil acidity and base status? These effects were found on the Oregon coast but not in a study in the Washington Cascade Range (Tarrant, 1961). What aspects of alder litter decomposition and what decomposition products are responsible for the phenomenon observed in our Oregon coast study? How much of the "missing" base can be accounted for in the standing crop? Once these questions have been answered, it will be possible to predict the extent and degree to which similar effects of alder on soil can be expected.

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Comparison of microbial populations between red alder and conifer soils[1]

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Abstract

Seasonal populations of molds and bacteria in the F layer and A11 soil horizon from stands of pure conifers, pure red alder, and conifer-alder mixtures near the Oregon coast were compared by dilution plating techniques. All organisms were generally more numerous in the F layer than in the A11 horizon. On this very moist site, populations of molds were lowest in spring, when the soil was extremely wet. In the F layer, Streptomyces *species, of particular interest due to their possible antagonism against root pathogens, consistently comprised a higher proportion of the total bacterial population of the mixed stand than of either pure alder or pure conifer stands.*

Introduction

The F layers and A11 horizons of forest soils harbor high populations of microorganisms active in carrying out a series of biochemical transformations essential to nutrition of trees and other plants. Evaluation of these transformations is important for comparing rates of nutrient release in different soils or under different environmental conditions. Moreover, the upper profile often appears crucial to establishment of seedlings.

Kivinen (1938) and Pearsall (1938) reported the relatively high acidity of soil under *Alnus* spp., and Hesselman (1917) found that nitrification occurred in acid woodland soil under alder stands. No information prior to this symposium has been reported about effects of red alder (*Alnus rubra* Bong.) on populations and activities of soil microbes in relation to soil fertility in either pure alder or mixed alder-conifer stands.

We have been studying the effects of red alder on forest soil near the Oregon coast on plots whose primary variable is tree species: pure red alder, pure conifer (*Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Picea sitchensis* (Bong.) Carr.), and alder mixed with conifers. The stands are now about 40 years old and have developed characteristic understories. Climate and soil parent material are similar for all plots.

Investigations have revealed pronounced differences in soil properties between three distinct plant associations, differences attributable almost entirely to influence of alder. Some of these, as presented in other papers in this symposium, are lower pH values, higher total nitrogen, and higher accumulation of ammonium and nitrate forms of nitrogen under red alder and red alder-conifer mixtures than under pure conifers. In this paper, we compare three types of stands in terms of seasonal populations of soil microbes.

Materials and Methods

Four sampling periods were scheduled from April 1962 to March 1963 to coincide with phenology of alder:

>April 1962 — leaves appeared and flowers opened
>July 1962 — flowers fell
>September 1962 — seeds ripened and leaf fall started
>March 1963 — leaf buds burst and understory vegetation
>   began rapid growth

For each period, a sample was composited from three subsamples of the F layer and A11 soil horizon of each plot and immediately screened through a sterilized ¼-inch sieve. Each subsample contained all material of each horizon from a 1-square-foot area demarcated by an iron sampling frame. Microbial analyses were made from triplicate plates of appropriate dilutions of the sieved fresh soils poured with peptone-glucose agar, acidified to pH 4.0 for molds, and with sodium-albuminate agar, pH 7.2, for bacteria and *Streptomyces.* Incubation was at 28 C. Counts were made after 3 days for molds and after 15 days for bacteria and *Streptomyces.*

Results

MOLDS

F layers. — Fluctuation of molds is shown in Fig. 1. Under pure alder, counts ranged from about 100 thousand per gram of soil in April to 380 thousand in July. Numbers under pure conifers changed from 100 to 700 thousand, with the lowest count in April and the highest in March. Trends under the pure alder and pure conifers were roughly parallel, the numbers decreasing from March to April, increasing in July, and finally decreasing in September. Numbers of molds in the F layer of the mixed stand changed little, increasing only slightly from March to September.

All horizons. — Molds fluctuated in the upper mineral soil in the same pattern under all three stands (Fig. 2). Highest numbers occurred in July and lowest in September. The counts varied from 55 to 180 thousand under pure alder, 135 to 300 thousand under pure conifers, and 82 to 215 thousand in the mixed stand.

Mold counts under the three stands were higher in the F layer than in the A11 horizon except under conifers, where molds were about 50 percent lower in the F layer than in the A11 horizon at the April and July samplings. A higher microbial population in the upper fermentative layer than in the
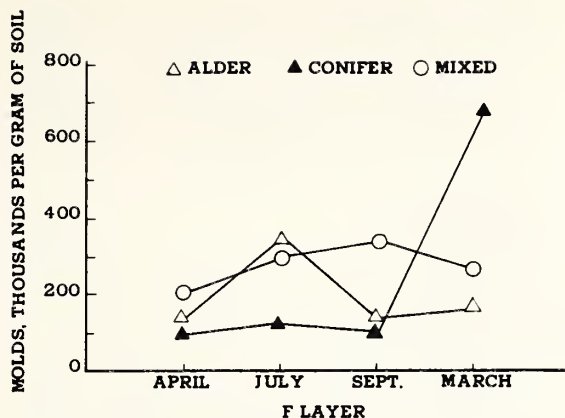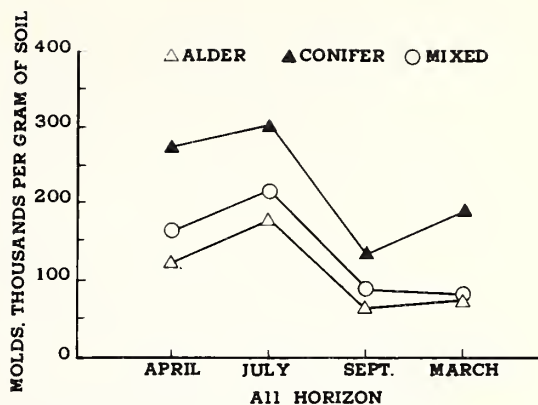
Figure 1. Seasonal changes in mold numbers.

Figure 2. Seasonal changes in mold numbers.

lower mineral layer was reported by Powers and Bollen (1935). These authors attributed the vertical difference in microbial populations to differences in nutrient values and physical conditions of the horizons.

Penicillium species predominated in all samples except the F layer under pure alder, where *Trichoderma* was more abundant (Table 1). In the March samples, *Trichoderma* was found only under alder. *Mucor* species were present in all samples except the alder F layer. *Aspergilli* appeared only in mixed-stand soil and the A11 horizon under pure conifers.

Studies on the relation of mold numbers and soil moisture content have shown that increase in soil moisture from the air-dry condition to near water-holding capacity will correspondingly increase the numbers (Jensen,

TABLE 1. Molds in F layers and A11 horizons (March 1963 samples) under alder, conifer, and mixed stands

				Molds					
Stand	Horizon	Water	pH	Total	Mucors	Aspergilli	Penicillia	Trichoderma	Others
		Percent		Thousands per g soil	- - - - - - - - - - - - - - - - - Percent - - - - - - - - - - - - - - - - -				
Alder	F	193	3.6	225	0	0	33	67	0
	All	98	3.9	73	13	0	40	37	10
Conifer	F	135	5.1	709	27	0	41	0	32
	All	105	5.3	195	19	8	39	0	34
Mixed	F	135	3.9	291	20	3	54	0	23
	All	90	4.3	79	23	5	49	0	23

1934). Because the area of our study has high annual rainfall and is effectively mulched by well-developed litter and F layers, the water supply could not often be a critical factor. On the contrary, reduction of mold counts in spring seemed more related to excess water, which could reduce aeration; generally, numbers of molds were inversely related to soil moisture.

BACTERIA

F layers. — Counts of bacteria (including *Streptomyces*) in pure alder fluctuated from 5.0 to 34.3 million per gram, being high in March and September and low in April and July (Fig. 3). Under pure conifers, the variation was similar, changing from 9.9 million in April to 37 million in September. Numbers in the mixed stand varied from 3.7 million in September to 16.7 million in July. Although the fluctuation in the mixed stand was much less than under pure stands of alder and conifers, the trend was opposite.

All horizons. — The trend in numbers of bacteria was similar in pure alder and pure conifers (Fig. 4), although the maximum for alder was in March and for conifers in July. Numbers ranged from 3.2 to 5.9 million under alder and from 3.1 to 11.3 million under pure conifers. In the mixed stand, on the other hand, numbers were lower and decreased to 1.7 million in September.

These numbers of bacteria are low, compared with numbers typical of field soils; such low numbers are generally characteristic of woodland soils (Salisbury, 1922). The data show that the bacterial population was always larger in the F layer than in the A11 horizon.

STREPTOMYCES

F layers. — The population of these higher bacteria, expressed as percent of total bacteria, in the F horizon under pure alder ranged from a low of 10 percent in March to a high of 52 percent in July, dropping to 35 percent in September (Fig. 5). A similar trend occurred in the mixed stand, where the highest value, 63 percent, was recorded in July. The lowest proportion of
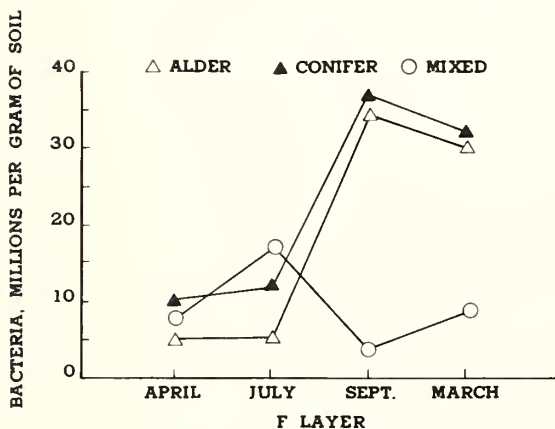

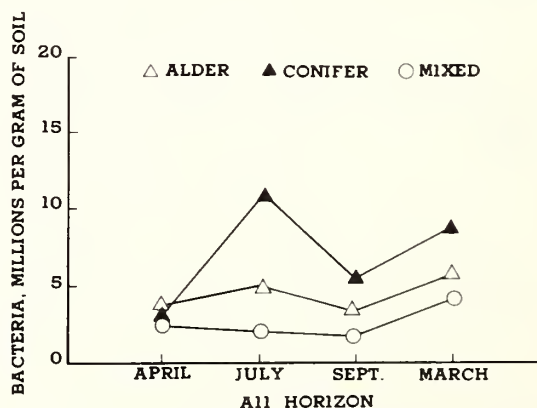Figure 3. Seasonal changes in bacterial numbers, including *Streptomyces*.

Figure 4. Seasonal changes in bacterial numbers, including *Streptomyces*.
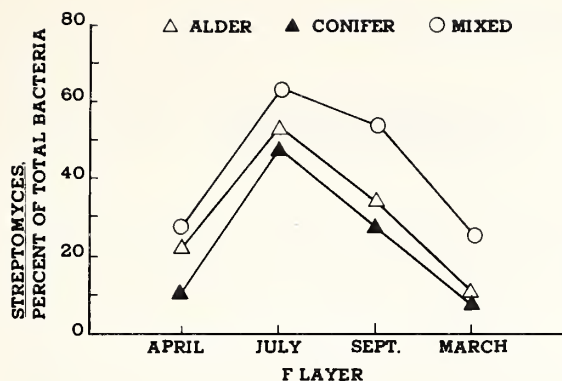
176

Figure 5. Seasonal changes in percentage
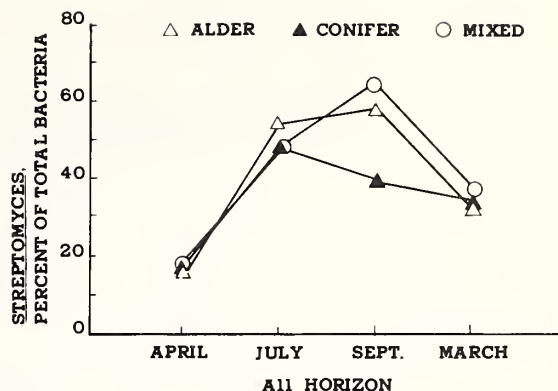of *Streptomyces*.

Figure 6. Seasonal changes in percentage
of *Streptomyces*.

Streptomyces, 10 percent, was found in April under pure conifers; it increased slightly thereafter but remained consistently lower than in the alder or mixed stands.

All horizons. – Similar trends of change in *Streptomyces* percentage (Fig. 6) occurred under pure alder and pure conifers. In the mixed stand, there was an increase from 25 percent in March to 65 percent in September. The highest value recorded under pure alder was 56 percent in September, when the maximum of 65 percent for the mixed stand was found. The lowest value, 20 percent, occurred under pure alder and pure conifers in April.

The data showed that the F layer of the mixed stand contained the highest proportion of *Streptomyces* at all seasons. Because many *Streptomyces* produce antibiotics, their preponderance in the alder-conifer association may be important in inhibiting fungal pathogens of conifer roots.

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Some ectotrophic mycorrhizae of *Alnus rubra*[1]

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Abstract

*Two forms of mycorrhizae predominated on root systems of red alder (*Alnus rubra *Bong.) in a pure stand near the Oregon coast. Detailed morphological studies, the first for this species, revealed distinct characteristic differences between the fungal symbionts. The great abundance of these mycorrhizae and their immediate influence on rhizosphere microbes could markedly affect the incidence of root disease.*

Introduction

Red alder is unique among the trees of the Pacific coast because its roots participate in either one of two major kinds of symbiosis: root nodules formed with nitrogen-fixing endophytes, presumably *Streptomyces*, and mycorrhizae formed with certain fungi. Nodulation not only increases available nitrogen but also profoundly affects other soil chemical and microbiological properties (Tarrant, 1961; Chen, 1965). The mycorrhizal fungi increase alder's nutrient-absorbing capability and affect it in other, less understood ways. Both kinds of symbiosis bear possible implications for minimizing incidence of root diseases when red alder is a component of forest stands (Zak, 1964; Li et al., 1967; Marx and Davey, 1967).

Our interest in rhizosphere phenomena of red alder led us to investigate its mycorrhizae in a pure stand about 40 years old near the northern Oregon coast in the Cascade Head Experimental Forest (maintained by the U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station). Vegetation, soils, and soil microbial activity in this stand are described in preceding papers of this symposium.

Methods and Materials

Mycorrhizae collected in spring and autumn 1965 were cleaned ultrasonically, fixed in a chrome-acetic acid solution, paraffin-embedded, sectioned at 8 to 10µ thickness, and stained with safranin-fast green. Fresh, whole specimens were saved for examination of gross morphology.

Nonmycorrhizal rootlets, desired as a base for evaluating effects of mycorrhizal infection on rootlet anatomy, could not be found in the stand.

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Accordingly, red alder seeds were surface-sterilized (Neal et al., 1967), germinated, and grown in pure culture to obtain infection-free roots.

Rootlet Anatomy and Morphology

The nonmycorrhizal rootlets had an epidermis of cells 5 to 10 x 8 to 16μ in cross-sectional dimensions (Fig.1A). Root hairs 6 to 9μ broad originated sporadically from this outer layer of cells (Fig. 1B). Cortical cells underlying the epidermis ranged from 15 to 27 x 15 to 35μ in diameter, and endodermal cells from 3 to 7 x 7 to 12μ. The xylem was monarch.

Two forms of alder mycorrhizae predominated in the collections. A third form occurred only infrequently, so it was not included in the study. We found no mycorrhizae formed with the fungus *Cenococcum graniforme* (Sow.) Ferd. et Winge, the only type heretofore reported for red alder (Trappe, 1964).

One common form of mycorrhizae, comprising about 40 percent of those collected, was generally clavate with a dark-brown, distinctively roughened fungal mantle (Fig. 2, left) which was commonly ruptured by apical growth of the enclosed rootlet (Fig. 2, middle). This mantle sloughed off when roots were removed from the soil.

Two layers of tissue comprised the mantle (Fig. 3, left), which totaled 40 to 60μ in thickness. The outermost layer, 30 to 45μ thick, was formed of irregular, more or less isodiametric, thick-walled cells 8 to 12μ broad (Fig. 3, left A). Irregular collapse of the peripheral cells of this layer accounts for the mycorrhiza's surface roughness. The inner mantle layer, 10 to 15μ thick, was composed of thin-walled hyphae 2 to 5μ in diameter, aligned predominantly along the root axis (Fig. 3, left B). The Hartig net penetrated only the epidermis (Fig. 3, left C), separating epidermal cells by one layer of hyphae 1.5 to 2.5μ thick.

The outermost root cells ranged from 15 to 27μ x 11 to 20μ in cross-sectional diameter; cortical cells, 30 to 85μ x 30 to 40μ; and endodermal cells, 10 to 20μ. The xylem was triarch.
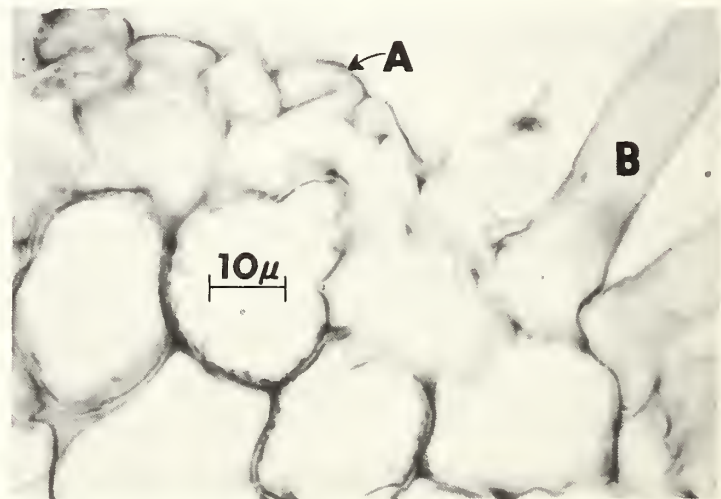
Figure 1. Cross section of nonmycorrhizal red alder root tip: A, epidermis; B, root hair.
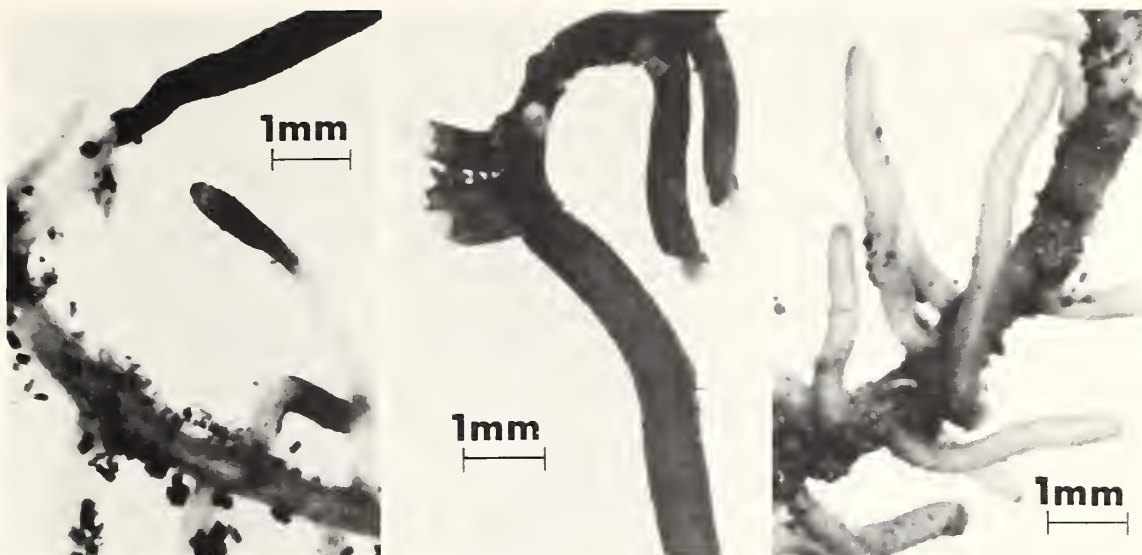
Figure 2. (Left) Clavate red alder mycorrhiza with dark-brown fungal mantle. (Middle) Mantles of dark-brown mycorrhizae ruptured by apical growth of enclosed rootlet. (Right) Red alder mycorrhiza with pale-brown, glabrous mantle.

Septate hyphae, averaging about 5 μ in diameter and having walls about 1 μ thick, sometimes originated from turgid cells at the mantle surface (Fig. 3, middle). Clamp connections were present at some septa of these hyphae. Therefore, the fungus was a Basidiomycete.
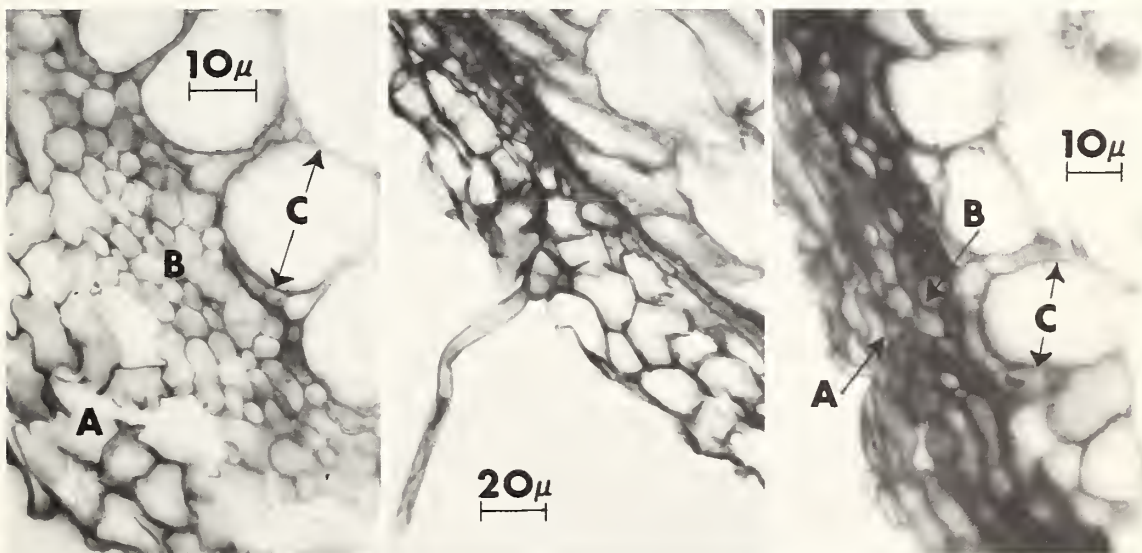
Figure 3. (Left) Cross section of mantle and outer root cortex of dark-brown, clavate, red alder mycorrhiza: A, outer mantle layer; B, inner mantle layer; C, Hartig net. (Middle) Longitudinal section showing hypha originating from outer mantle cell of dark-brown mycorrhiza. (Right) Cross section of mantle and outer root cortex of pale, glabrous mycorrhiza: A, single-layered mantle; B, opaque, amorphous layer; C, Hartig net.

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The other common form of mycorrhiza (Fig. 2, right), comprising about 50 percent of those collected, was pale brown and glabrous. No mycorrhizal mantle was obviously present under low-power magnification, but side-by-side comparison with uninfected roots revealed distinct differences, especially in color.

The mantle, 12 to 25 μ thick, constituted a single-layered prosenchyma tightly adhering to the ·rootlet surface and aligned predominantly with the root axis (Fig. 3, right A). Mantle hyphae were 2 to 2.5 μ in diameter.

A single-layered Hartig net (Fig. 3, right C), 2 to 3 μ broad, sporadically penetrated the rootlet epidermis. Consequently, we consider this mycorrhiza weakly ectotrophic, even though a true Hartig net was lacking from much of the fungus-root interface. A layer of opaque, amorphous, red-stained material, perhaps tannin, was often present between the epidermis and the mycorrhizal mantle (Fig. 3, right B).

The outermost root cells varied from 10 to 30 μ in diameter; cortical cells, 30 to 65 μ ; and endodermal cells 9 to 18 μ . The xylem was triarch.

We could not classify the fungus participating in this form of mycorrhiza for lack of distinctive, morphological characteristics.

Discussion

The lack of root hairs on the mycorrhizae is the only anatomical change that can be attributed to mycorrhizal infection, considering that the mycorrhizae were collected from 40-year-old trees and the nonmycorrhizal rootlets from seedlings grown in pure culture. The outermost tier of root cells on the mycorrhizae, though smaller than the cortical cells, did not appear to be a typical epidermis in comparison with that of nonmycorrhizal roots. We cannot say, however, whether this difference is due to mycorrhizal infection or whether it merely reflects the difference in age and environment of the mycorrhizal versus nonmycorrhizal roots. Masui (1926) illustrated a similar phenomenon in his paper on mycorrhizae of Japanese alders, as did Klečka and Vukolov (1935) for *Alnus incana* (L.) Moench.

No counterpart of the rough, brown mycorrhiza of red alder has been reported for other *Alnus* species, but the glabrous form resembles a mycorrhiza of *Alnus incana* in Europe (Klečka and Vukolov, 1935). All have a Hartig net that penetrates only the outer tier of root cells as did several other forms of ectotrophic mycorrhizae described for Japanese *Alnus* species (Masui, 1926). This shallow penetration by the Hartig net appears to be characteristic of *Alnus* species, in contrast to the deeper penetration frequent in ectotrophic mycorrhizae of many other tree species.

Sporocarps of fungi fruiting in the stand were collected over the course of 18 months. Of the 30 terrestrial species found, only 5 were likely to form mycorrhizae: *Alpovah cinnamomeus* Dodge, *Hymenogaster alnicola* A. H. Smith, *Lactarius obscuratus* (Lasch) Fr., and two *Inocybe* species. We cannot say with certainty if any of these is the fungal symbiont of either of the mycorrhizae described. *Lactarius obscuratus*, however, fruits abundantly in

the stand and has basal hyphae similar to those forming the mantle of the glabrous mycorrhiza.

Different forms of mycorrhizae can harbor populations of rhizosphere organisms which differ distinctly in certain physiological activities (Neal et al., 1964 and 1968). Undoubtedly, the two abundant forms of red alder mycorrhizae described here strongly influence rhizosphere populations and possibly the general soil microflora. Through this influence, the mycorrhizae could markedly affect the incidence of root disease.

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Nodule endophytes in the genus *Alnus*

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Abstract

The Alnus glutinosa *endophyte symbiosed satisfactorily with two other European alders (*A. cordata *and* A. incana*), but the* A. rubra *endophyte performed less satisfactorily on the European host species, mainly because of a delay in nodule formation. This provides further evidence that the endophytes of* Alnus *species from different geographical regions may not be identical. This regional specialization is particularly likely in such a widely dispersed genus as* Alnus.

Introduction

Although further investigation of some aspects of non-legume root nodule plants is hindered by the present lack of pure cultures of the nodule endophytes, progress is possible on the question of the extent to which there is specificity between the partners in these symbioses. Even here it would be much more desirable to start with pure cultures of the endophytes rather than with nodules containing them, but until this ideal is attained we must make do with crushed nodule inocula.

At the generic level, *Alnus, Myrica, Casuarina, Coriaria,* and *Ceanothus,* all of different families, are not usually considered cross-inoculable. This belief is based to some extent on actual tests (Bond, 1963), but also on circumstantial evidence; for example, there is no record of *Ceanothus* or *Coriaria* species forming nodules in British soils, though the *A. glutinosa* organism occurs widely in such soils. On the other hand, full cross-inoculation has been demonstrated between the genera *Elaeagnus, Shepherdia,* and *Hippophaë* (Bond, 1963; Moore, 1964) which together comprise the family Elaeagnaceae, but there is no record of cross-inoculation between these genera and others listed above. The possibility of inter-generic infection involving species more recently discovered to be nodule-bearing is so far unexplored. Thus one wonders whether cross-infection is possible between *Ceanothus* and *Discaria,* both members of the Rhamnaceae, or between *Dryas, Purshia,* and *Cercocarpus,* belonging to the Rosaceae.

Cross-infection within a given genus of host plants has received little attention until recently. Mowry (1933) showed that cross-inoculation was readily obtained among nine species of *Casuarina* growing as introductions in Florida, although it might be pointed out that at least two of his specific names are generally considered to be synonyms. Actually, *Casuarina* is a genus in which cross-inoculation at the species level might be expected, since the

genus is endemic to Australia and the Pacific Islands. Roberg (1938) also examined a group of plant species native to a particular area, namely the European species *Alnus glutinosa* (L.) Gaertn., *A. incana* (L.) Willd., *A. cordata* (Lois.) Desf., and *A. viridis* Regel, and found cross-infection to occur between the species.

On the other hand, Bond (1962) found that seedlings of the Asian species, *Coriaria japonica* A. Gray, failed to form nodules when grown in soil collected from around bushes of the Spanish species *C. myrtifolia* L., whereas seedlings of the latter species showed good nodulation in the same soil. In the genus *Myrica*, Gardner and Bond (1966) reported that nodules forming on the North American species *M. cerifera* L. and the South African species *M. cordifolia* L. in response to inoculation from *M. gale* L. conveyed little benefit to the host plant. After a reexamination of *M. cerifera* plants inoculated in the same way, Bond (1967) reported that large numbers of minute nodule-clusters, scarcely visible to the naked eye, were present. Rodriguez-Barrueco (1966) had previously reported a similar situation in *Alnus jorullensis* H. B. & K. Plants of this species inoculated from *A. jorullensis* nodules grew vigorously and fixed abundant nitrogen, while plants inoculated from *A. glutinosa* formed 12 times as many nodules, all of which remained small and fixed little nitrogen (Fig. 1). Becking (1966) reported that only about a fourth of the plants of the North American species, *Alnus rubra*, formed nodules in response to inoculation from *A. glutinosa*, and that these nodules did not fix nitrogen very vigorously.

EXPERIMENTAL

In the study reported here, the effects of inoculating three European species of *Alnus*, namely *A. glutinosa*, *A. incana*, and *A. cordata*, from (a) nodules of *A. glutinosa* and (b) from nodules of *A. rubra* Bong. have been compared. Seedlings of the three host species were raised from surface-sterilized seed (sown in April 1966) and transplanted into water culture in a nitrogen-free culture solution, pH 5.0. For inoculation purposes, nodules of *A. glutinosa* were obtained from a large plant of that species growing in the greenhouse; this plant had been inoculated originally from field nodules of the same species. Nodules of *A. rubra* were received in June 1966 by airmail from Portland, Oregon, from the Pacific Northwest Forest and Range Experiment Station; they were still attached to short lengths of roots. Inocula were prepared by grinding nodules in water in the proportion of 10 g to 100 ml, two drops of such inoculum being applied to the root system of a young plant. Full precautions were taken to prevent unintended contamination of plants by nodule organisms; some 20 uninoculated control plants remained without nodules throughout the experiment.

Subsequent observations showed that although all plants of all species inoculated from *A. glutinosa* were nodulated 3 weeks after inoculation, very few nodules had been induced by the *A. rubra* inoculum by that time. *A. glutinosa* plants inoculated from *A. rubra* were all nodulated after 5 weeks, but it was 8 weeks after inoculation before all plants of *A. cordata* and *A. incana* nodulated. Plant responses indicated that nodules induced by *A.*

Figure 1. Plants of *Alnus jorullensis* after 21 weeks' growth in nitrogen-free culture solution. Left to right: nodulated plants (*A. glutinosa* inoculum), non-nodulated control plants, nodulated plants (*A. jorullensis* inoculum). (For scale, note that the front edge of the teak jar covers measured 18 cm.) Reproduced with permission from Phyton, Vol. 23, 1966.

rubra inoculum were effective in fixation. However, because of the delay in nodule formation, plant growth was considerably inferior, on the average, to that of plants of the same species inoculated from *A. glutinosa*, with which vigorous fixation was evidently associated. These findings are illustrated in Fig. 2 and further substantiated by the data obtained at harvest, 3 months after inoculation (Table 1). Taking mean nitrogen fixed (obtained by subtracting the nitrogen content per control plant from that of the nodulated plant) as a measure of the success of the symbiosis, and expressing nitrogen fixed per plant inoculated from *A. rubra* as a percentage of the corresponding figure for plants inoculated from *A. glutinosa*, the following results are obtained:

For	*A. glutinosa*	32%
For	*A. cordata*	6%
For	*A. incana*	19%

Obviously the symbioses were much less satisfactory where *A. rubra* was used, especially in *A. cordata* and *A. incana*.

The above conclusions are based on mean values. A feature of the plants inoculated from *A. rubra* nodules was the unevenness within a given treatment, those plants which nodulated relatively early becoming in due course considerably stronger than the other plants. This feature is shown in Fig. 2C, and is verified by the standard deviations of mean dry weights (expressed as percentages) included in Table 1. These confirm that the variation was substantially greater where *A. rubra* inoculum had been used. In *A. incana* the dry weight of the largest plant in the series inoculated from *A. rubra* actually
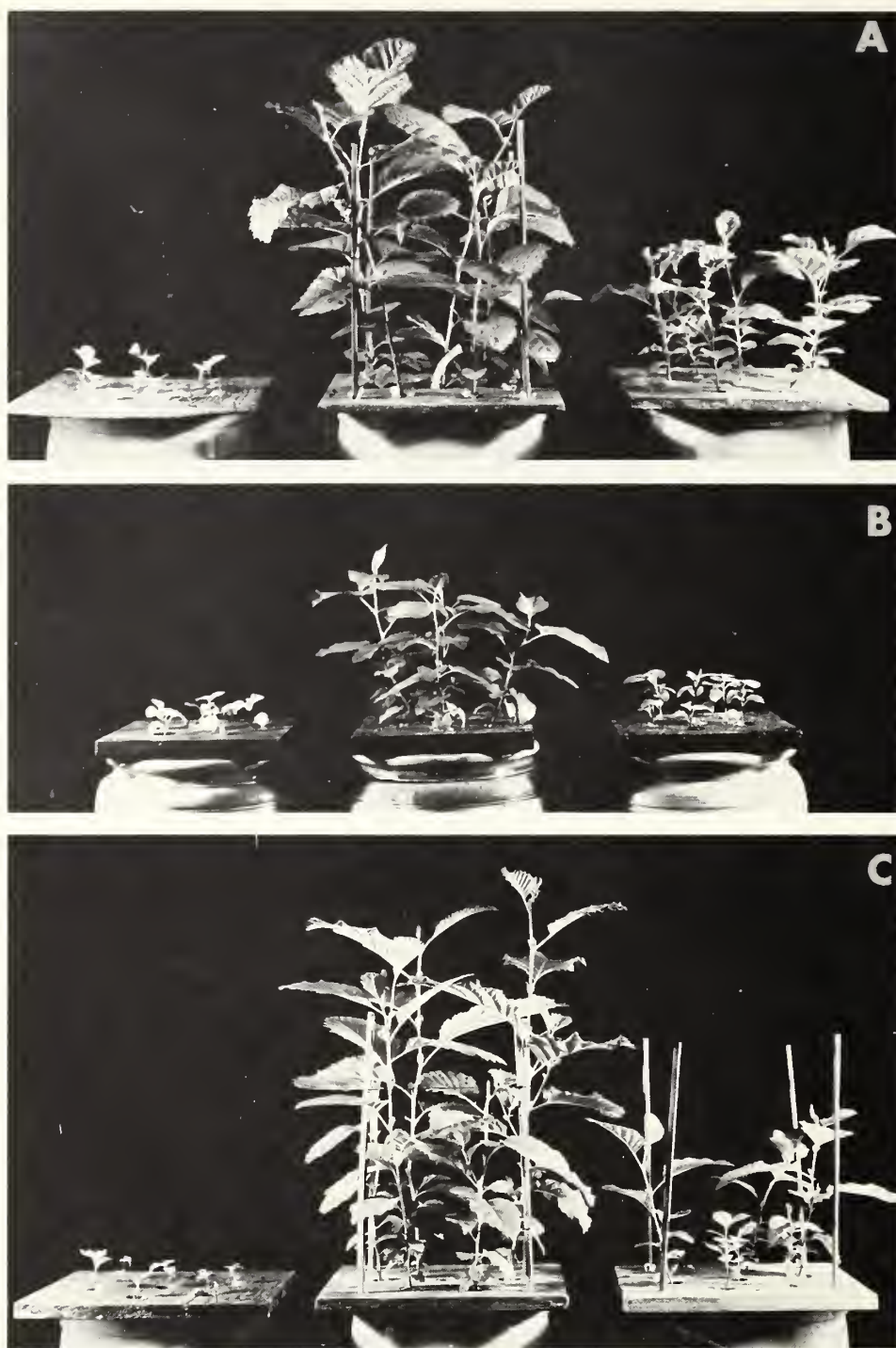
Figure 2. A, plants of *Alnus glutinosa*; B, of *A. cordata*; and C, of *A. incana*; all after 3 months' growth, from inoculation, in nitrogen-free culture solution. Left-hand jars: non-nodulated control plants. Center jars: plants inoculated from *A. glutinosa* nodules. Right-hand jars: plants inoculated from *A. rubra* nodules. (Scale same for all species. The front edge of the teak jar covers in A and C measured 18 cm, 13 cm in B.)

TABLE 1. Harvest data for *Alnus* species inoculated from *A. glutinosa* or *A. rubra,* means per plant

Host plant	Source of inoculum	Total no. of plants	Nodule dry weight	Dry weight, whole plant	Standard deviation[1]	N per plant
			Mg.	Grams	Percent	Mg.
A. glutinosa	*A. glutinosa*	5[2]	72	1.899	39	40.9
A. cordata	*A. glutinosa*	16	39	.749	27	15.4
A. incana	*A. glutinosa*	20	76	1.922	50	47.6
A. glutinosa	*A. rubra*	25	24	.546	55	13.4
A. cordata	*A. rubra*	23	3	.078	50	1.2
A. incana	*A. rubra*	25	12	.348	143	9.1
A. glutinosa	No inoculation	7	-	.043		.3
A. cordata	No inoculation	6	-	.041		.3
A. incana	No inoculation	6	-	.029		.3

[1] *Standard deviation is expressed as a percent of the mean dry weight.*

[2] *This rather small number of harvested plants was drawn from a large block of similar plants, the rest of which were required for another purpose. It is certain that if more plants had been harvested, the mean data would have been little different from those shown above.*

exceeded the mean dry weight of the corresponding plants inoculated from *A. glutinosa*, whereas other plants scarcely exceeded the non-nodulated control plants in their growth.

Discussion

It is clear that the *A. glutinosa* endophyte was able to induce nodulation in *A. cordata* and *A. incana* plants with the same facility as it did in *A. glutinosa*, since all plants were nodulated within 3 weeks. This conclusion agrees with those of Roberg (1938) and Becking (1966). The present study has further shown that these nodules on *A. cordata* and *A. incana* fixed nitrogen efficiently, as indicated by (1) the satisfactory color of the leaves of the plants despite the lack of nitrogen in the initial rooting medium, and (2) by the high level of nitrogen in the whole plant dry matter (2.056 percent for *A. cordata* and 2.476 percent for *A. incana*). Thus there is no evidence of host plant-endophyte specialization among these European alders. It is possible that under natural conditions these different plant species are frequently or always in symbiosis with one and the same endophyte.

Although nodule formation was generally slower on the three host species when *A. rubra* inoculum was applied, the nodules eventually formed appeared to be effective in fixation (Table 2). Taking each species in turn, it is clear that fixation per unit weight of dry nodule was of the same order regardless of inoculum. Thus the inferior performance of symbioses involving the *A. rubra* endophyte was due largely or entirely to the delay in nodulation. This is evidence of a lack of adaptation between the endophyte and the host plants. On the average, its degree varied between different host species, being least in *A. glutinosa* and greatest in *A. cordata*. There was, however, much plant-to-plant variation within a species, possibly owing to genetic differences.

In considering these results of inoculation from *A. rubra* nodules, it should be remembered that the nodules used had been excised from the trees 3 days prior to use (though they had remained attached to lengths of roots), whereas the *A. glutinosa* nodules used for preparing the alternative inoculum were freshly detached. This is not thought to have affected the comparison materially because (1) many nodule samples have been used in this laboratory with complete success after long journeys by air, (2) large nodule clusters of non-legumes collected locally have been stored for more than 3 days without any loss of infective power by the endophyte, and (3) the *A. rubra* inoculum varied in its effect between the three host species.

One of us (G. B.) had grown plants of *A. glutinosa* inoculated from *A. rubra* in 1957, following the same procedure and with exactly the same result as in the present trials — some plants grew quite strongly, others less so. On the earlier occasion it was assumed that the presence of these weaker plants was due to mutual shading between the plants, and the performance was assessed on the basis of the stronger plants and judged to have been satisfactory. This conclusion was quoted by Tarrant and Miller (1963). In the present trials, spacing was better, and our belief is now that all plants should be included in assessing the overall effectiveness of the symbiosis.

TABLE 2. Efficiency of nodules in fixation[1]

Host plant	Source of inoculum	Mg N fixed per g nodule dry matter formed
A. glutinosa	*A. glutinosa*	550
A. cordata	*A. glutinosa*	387
A. incana	*A. glutinosa*	622
A. glutinosa	*A. rubra*	546
A. cordata	*A. rubra*	300
A. incana	*A. rubra*	733

[1]*Calculated from data presented in Table 1.*

The situation revealed in this present study is quite different from that found previously in plants of *A. jorullensis* and of *Myrica* species inoculated with a 'foreign' endophyte (see Introduction). There a lack of adaptation between host plant and endophyte revealed itself by the formation of very numerous, small nodules fixing little or no nitrogen, very reminiscent of a condition frequently shown in legumes when "ineffective" rhizobia are present, suggesting that nodulation in the nonlegumes is subject to the same hormonal control demonstrated for legumes (Nutman, 1949). In the present study the nodule clusters were not counted, but it is certain that there was no tendency for the number of clusters to be greater when *A. rubra* inoculum had been used, and moreover the nodules were effective in fixation.

Finally it may be noted again that Becking (1966) reported that the symbiosis between the *A. glutinosa* endophyte and *A. rubra* plants (i.e. the reciprocal of one of the combinations tested above) was also not completely satisfactory.

Thus the present study provides further evidence that the endophytes normally associated with different species of *Alnus* may not be identical. It is an obvious possibility that the association over very long periods of time of a given endophyte with a particular species or a group of species growing in a distinct geographical area, will result in adaptations arising which may prevent satisfactory symbiosis with 'foreign' host species, differing in physiological and morphological characteristics from the usual host species. A widely dispersed genus such as *Alnus*, with distinct species occurring in several continents, is particularly liable to show such endophyte specialization.

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Some effects of alder
on the forest environment[1]

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Abstract

*Evidence from many studies indicates that alder (*Alnus *spp.) has a potential relation to forestry similar to that of legumes to agriculture.* Alnus, *together with seven other genera of woody, nitrogen-fixing angiospermous plants, is an important source of combined nitrogen for plants in general, especially in cool climates.*

The soil-improving function of alder has been employed widely in rehabilitating mine spoils in Great Britain, the Netherlands, Germany, and, to a lesser extent, the United States. Alder is used routinely to stabilize recent flood deposits and landslide areas in Rumania, Czechoslovakia, and Germany. Other areas of the northern hemisphere in which alder has been used successfully to improve soil fertility are the U.S.S.R., Italy, Denmark, Japan, and Taiwan.

The degree of nitrogen fixation in nodules of alder considerably exceeds that in legume nodules. Alder is perhaps most effective as a nitrogen-fixing plant when soil nitrogen is low. Nitrogen accumulation, ranging from 60 to 209 kg per ha per year, has been reported for newly developing soils bared by recent glacier retreat or from pot tests wherein nitrogen was lacking.

Although most species of Alnus *do not attain a size and form that make them usable for timber, they do have considerable value in improving growth of timber tree species with which they are associated. Growth of trees of the following genera has been shown to increase under the influence of associated alder:* Fraxinus, Liquidambar, Liriodendron, Picea, Pinus, Platanus, Populus, *and* Pseudotsuga.

We have substantial evidence of the soil-improving quality of many species of Alnus, *yet study of alder ecology and its application to silvicultural practice is only recently becoming intensified. Perhaps the strong encouragement given to increased research on all aspects of nitrogen fixation under the International Biological Program will speed progress toward our learning to capitalize on the substantial nitrogen-fixing capacity of the genus* Alnus. *Especially in Pacific Northwest United States, where wild forests are rapidly being converted to intensively managed systems, the demonstrated capacity of* Alnus *to enhance soil fertility and forest productivity appears to be a biological tool that we must learn to use effectively.*

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[1]*Material discussed in this abstract will be presented in greater detail in the forthcoming Proceedings of the Eighth International Congress of Soil Science.*

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Resistance of *Alnus rubra* to infection by the root rot fungus *Poria weirii*

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Abstract

Attempts at inoculating red alder roots with cultures of Poria weirii *plus studies of excavated root systems indicated that alder is not susceptible to sustained infection by this pathogen.*

Inoculation experiments. – One root each of 15 *Alnus rubra* Bong. trees were inoculated to ascertain their susceptibility to infection by the root rot fungus *Poria weirii* Murr. Inoculum consisted of previously boiled alder stem sections, approximately 6 cm in length and 4 cm in diameter, upon which the fungus had been growing in pure culture for 3 months. The inoculum was tied in contact with the roots, the inoculation site was then covered with polyethylene, and the soil replaced to its original level.

The inoculum was removed after being in contact with the roots for 18 months. In every instance a limited growth of mycelium was present on the roots; the maximum extent of mycelial growth from the inoculum block was only 4 cm. In only one instance had the fungus been successful in penetrating the bark; growth of mycelium in the wood was 0.1 cm.

Natural infection. – In a further attempt to determine the susceptibility of red alder to infection by *Poria weirii* the roots of three trees growing in intimate contact with infected roots of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were excavated and sectioned. Portions of the roots of each alder were closely appressed to infected Douglas-fir roots, sufficiently so, in some instances, to have disrupted the bark.

Poria weirii mycelium was present on the bark surface of most of the alder roots in the vicinity of the contacts with the Douglas-fir roots. In no instance, however, was there any evidence of fungal development in the woody tissues; attempts to isolate the fungus from the alder wood were not successful.

On the influence of alder *(Alnus inokumae)* on soil properties in northern Japan[1]

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Introduction

Alder *(Alnus inokumae)* is widely distributed in the northern and middle parts of Japan, especially in Aomori Prefecture (Murai, 1962). Since ancient times, alder has been recognized as a soil-improving tree in Aomori district, where cutover alder sites are usually utilized as farmland.

Growth of alder is very rapid, and the cutting age for utilization is generally 15-20 years. Recently, it has been recognized as a fast-growing tree species in northern Japan, and alder plantations are gradually increasing.

Alder forms root nodules and can fix nitrogen symbiotically. Accordingly, it is believed that alder can grow vigorously even on infertile lands and simultaneously fertilize them (Uemura, 1961). However, there are some doubts about such beliefs, especially from the viewpoint of soil properties. Consequently, the author investigated the relation between growth of alder and soil condition from 1962 to 1964. This paper discusses the influence of alder on soil properties.

Results

Comparison of Soil Properties Under Neighboring Forests of Alder and of Other Species

In southeastern parts of Aomori district, where alder is widely distributed, soil parent materials are derived from Towada volcanic ash. The soils are classed as black soil (Ando soil), with loam or sandy loam textures, including pumice. Plots were examined in alder forest and in neighboring chestnut *(Castanea crenata)* and Japanese cedar *(Cryptomeria japonica)* forests situated on hilly convex topography.

Morphology of lower layers (below about 20 cm) of each soil is somewhat different, but that of surface layers is generally similar (Fig.1). In alder soils the amounts of carbon, nitrogen and exchangeable calcium are lower and soil is more acid than in chestnut and Japanese cedar soils (Table 1). So, it appears that the alder forest soil is inferior to those of chestnut and Japanese cedar in chemical properties.

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[1]*Adapted from the following publication: Yamaya, Kōichi and Yanagiya, Kiyoko. 1966. Some considerations on the effects of soil-improving trees on* Alnus inokumae. *Annu. Rep. Tohoku Branch, Forest Exp. Sta. No. 7: 100-110, illus.*
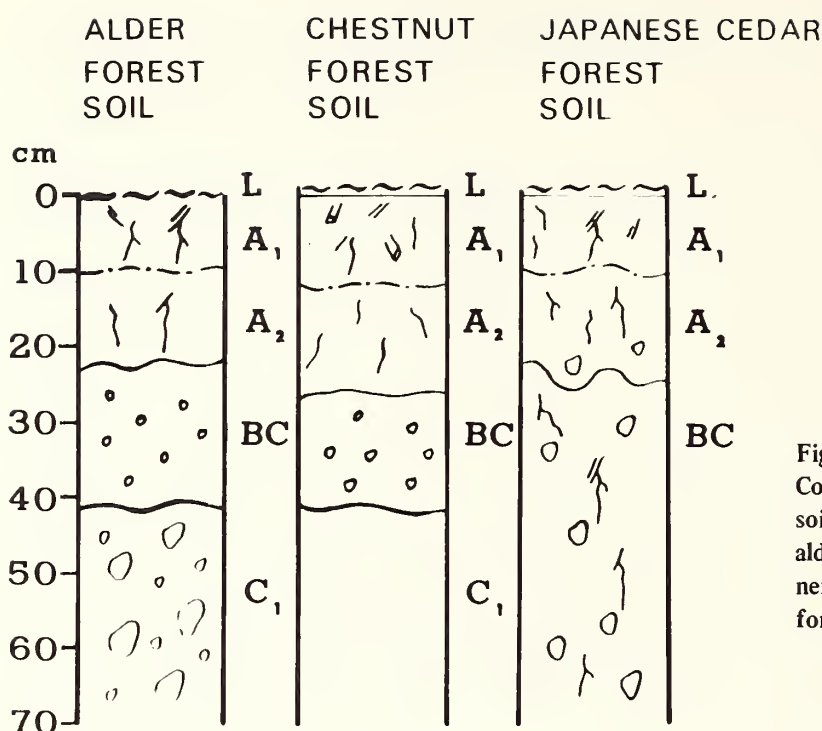
Figure 1. Comparison of soil profiles in alder and other neighboring forests.

In the alder soil, bulk density is greater and proportion of coarse pore space and permeability is lower than in the other soils (Table 2). Therefore, the alder forest soils are apparently also inferior to neighboring forest soils in physical properties.

Rate of Alder Leaf Decomposition

Fresh leaves of alder, collected in autumn, were air-dried and used in the laboratory and field experiments. Needle-leaves of Japanese cedar were similarly treated for use as a control.

Laboratory experiment. Each air-dried sample was coarsely pulverized, and a weighed amount of each was placed in a beaker and saturated with distilled water. Each beaker was then placed in a 27 C incubator for 30 and 90 days. After incubation treatment, each sample was ovendried and analyzed (Table 3).

Major differences between alder and Japanese cedar in decomposition rates during incubation cannot be recognized (Table 3). Degree of humification of decomposed residues increases according to length of incubation period; i.e., it is greater in order of 90 days > 30 days > original leaves. Also, alder leaves are humified faster than those of Japanese cedar.

Field experiment. A weighed amount of loamy volcanic soil, including only a little humus (substratum of nursery soil), was placed in porous pots of 25 cm diameter and 21 cm depth (Fig. 2). Air-dried leaves were then deposited on the soil surface, and the pots were covered with wire net. These pots were buried in the ground under natural red pine forest with their upper 10 cm exposed. The surface soil in the pine stand was similar to pot soil. The

TABLE 1. Chemical properties of soil under alder and under neighboring forests of chestnut and Japanese cedar

Forest	Soil[1]	Horizon	Carbon	Nitrogen	C/N	pH (H_2O)	Exch. acidity[2]	Hydro. acidity[3]	Exch. calcium
			Percent	*Percent*			y_1	y_1	*Meq/100g*
Alder	B1D	A1	5.8	0.51	11	4.25	9.3	91.4	4.02
		A2	1.1	.16	7	4.45	5.0	43.8	1.02
		BC	1.1	.12	9	5.50	1.2	21.2	1.52
Chestnut	B1D	A1	7.0	.53	13	5.55	.6	37.5	9.28
		A2	3.5	.33	11	5.35	1.8	28.8	1.16
Japanese cedar	B1D	A1	13.1	1.00	13	5.95	.6	36.3	22.14
		A2	5.6	.40	14	5.65	1.2	33.1	5.30
		BC	1.5	.16	9	5.65	.6	20.6	1.40

[1] *B1D is a moderately moist Ando soil.*
[2] *Exchange acidity is based on first titration of soil extract obtained using N KC1 solution with 0.1 N NaOH. The y_1 is cc/100 g.*
[3] *Hydrolytic acidity is based on a soil extract using calcium acetate solution. In early stages of acidification, soil acidity is more apparent with a measure of hydrolytic than with exchange acidity.*

TABLE 2. Physical properties of soil under alder and under neighboring forests of chestnut and Japanese cedar

Forest	Soil	Horizon	Bulk density	Composition of pores			Permeability	Proportion of 3 phases		
				Total	Coarse	Fine		Soil	Water	Air
				- - - - - - *Percent* - - - - - -			*cc/min*	- - - - - - *Percent* - - - - - -		
Alder	B1D	A1	0.50	79	28	51	38	20	38	42
		A2	.63	72	39	33	34	28	44	28
Chestnut	B1D	A1	.39	81	34	47	370	19	38	43
		A2	.60	74	38	36	62	27	38	35
Japanese cedar	B1D	A1	.32	84	35	49	405	16	39	45
		A2	.57	74	34	40	62	26	48	26
		BC	.48	77	38	39	114	23	46	31

TABLE 3. Comparison of leaf decomposition of alder and Japanese cedar

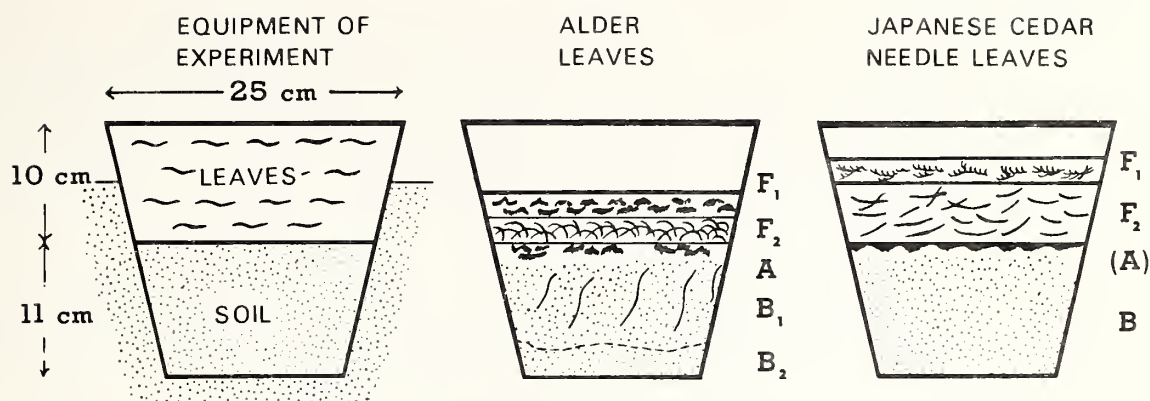| Treatment and tree species	Sample weight	Weight after decomposition	Amounts of decomposition	Rate of decomposition	Carbon	Nitrogen	C/N	Humic acid	Fulvic acid	$\frac{Ch}{Cf}$
	---------- Grams ----------			*--------- Percent ---------*				*---- Percent ----*		
Before treatment:										
Alder	—	—	—	—	48.4	3.24	15	3.71	7.97	0.46
Japanese cedar	—	—	—	—	51.7	.86	60	8.52	13.47	.63
Laboratory experiment:										
30 days:										
Alder	18.8	16.2	2.6	13.8	—	—	—	5.08	6.09	.83
Japanese cedar	19.0	16.5	2.5	13.1	—	—	—	9.50	10.40	.91
90 days:										
Alder	18.8	15.4	3.4	18.0	—	—	—	6.02	5.59	1.07
Japanese cedar	19.0	15.7	3.3	17.3	—	—	—	11.27	7.92	1.24
Field experiment:										
May~,Alder:										
F₁	250	47	151	60	46.6	3.88	12	7.50	4.04	1.86
F₂		52			43.9	3.49	13	9.10	3.66	2.49
Nov., Cedar:										
F₁	250	49	101	40	49.2	1.46	34	8.29	4.65	1.78
F₂		100			45.2	1.48	31	5.28	3.43	1.54

Figure 2. Comparison of leaf decomposition of alder and Japanese cedar.

pots were left untreated and exposed from May to November. At the end of November, the pots were dug out, and the condition of leaves and leaf-decomposition was examined. After weighing, a sample of the decomposed fraction was analyzed.

By the end of November the original leaves had undergone a clear morphological change into F_1 and F_2 layers (Fig. 2). Changes of alder leaves were greater than those of Japanese cedar.

Decomposition rate of the alder leaves is faster than that of the Japanese cedar leaves, and the degree of humification of decomposed leaves is also higher for alder than for cedar (Table 3). The author believes that this is characteristic of alder leaves, which are rich in nitrogen.

The decomposition rate under field conditions is much faster than in the laboratory (Table 3) perhaps due to the influence of soil fauna. By the end of November when the author examined the decomposition of leaves with the naked eye, there were a large number of spring-tails, centipedes, earthworms, etc. in decayed litter, especially in that of alder. Indeed, in November decomposed leaves of alder remained only as fibrous veins with most of the mesophyll having disappeared. The author believes that this is because the leaves of alder are rich in nitrogen and, consequently, are easily attacked by soil fauna. Accordingly, in the process of leaf-decomposition leaves are first broken and decomposed by the activity of soil fauna, and second, humified by soil microbes.

Influence of Alder Leaves on Soil Properties

As stated above, leaves of alder are rich in nitrogen and easily decomposed, so the degree of humification of decayed leaves is considerable. The author would next like to describe the effect of this alder leaf-decomposition on soil properties.

From the results of field experiment (Fig. 2), it is seen that in Japanese cedar pots, humus substances remain as a filmy accumulation on the surface of the loamy volcanic soil, but in alder pots, a crumb-like A is formed on the surface, and the original humus-poor soil is divided into B1 and B2 horizons by infiltration of the humus. This tendency is apparent from the data in

Table 4. Amounts of carbon, nitrogen and alkali-dissolved humus are greater in alder pots than in Japanese cedar pots. Exchangeable calcium contents are also greater in the former than in the latter. Despite this, soil in alder pots is more acid. It is interesting that soil acidity in Japanese cedar pots is weaker than that of the original soil. Perhaps the supply of bases originating in leaf-decomposition has a stronger influence than the supply of humus matter.

The author has also observed the effect of an alder plantation on fresh volcanic ash soil. Soil morphology under 20-year-old alder forest in the southeastern part of Aomori Prefecture is illustrated in Fig. 3. It is seen that A1 and A2 horizons have formed in the upper layers of fresh volcanic ash by humus accumulation. Furthermore, from data in Table 4, it is found that, as mentioned above, the amounts of carbon, nitrogen and exchangeable calcium have greatly increased over that found in fresh volcanic ash soil, and soil acidity has become stronger 20 years after planting of alder.

Discussion

Alder has been utilized for soil-improvement and forestry conservation since ancient time, and moreover, in recent years has been widely planted as a fast-growing timber species. However, the relation between growth of alder

TABLE 4. Changes of soil properties owing to the leaf decomposition of alder

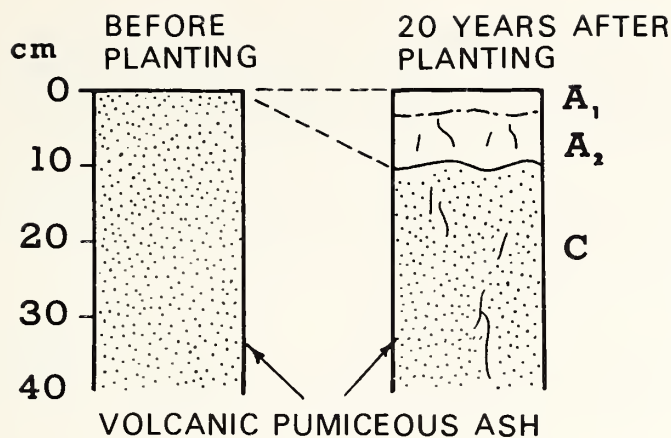| Location	Division	Horizon	Carbon	Nitrogen	pH (H_2O)	Exch. acidity	Hydro. acidity	Exch. calcium	Humic acid	Fulvic acid	$\frac{Ch}{Cf}$
			Percent	Percent		y_1	y_1	Meq	Percent	Percent	
Pot experiment (Morioka)	Original soil (Vol. ash)	—	0.6	0.07	6.40	0.6	13.8	6.74	0.07	0.13	0.54
	Alder pot	A	5.5	.43	5.75	1.3	43.8	15.92	1.20	1.40	.86
		B_1	2.6	.22	5.80	1.3	35.6	8.39	.43	.77	.56
		B_2	1.3	.13	6.15	.6	18.8	5.72	.17	.36	.47
	J. Cedar pot	(A)	2.5	.19	7.05	.6	10.6	12.61	.27	.67	.40
		B	1.2	.11	6.90	.6	13.1	7.54	.13	.35	.37
Plantation (Aomori district)	Original soil (Vol. ash)	—	.05	.02	6.85	.6	11.3	2.92	–	–	–
	Alder for. soil, 20 years after plant.	A_1	7.9	.65	4.70	1.9	55.7	11.96	–	–	–
		A_2	2.6	.23	4.45	4.4	40.7	3.18	–	–	–
		C	.3	.04	5.75	1.3	17.5	3.84	–	–	–

Figure 3. Soil formation on volcanic pumiceous ash owing to the planting of alder (about 20 years after planting).

and soil condition has not yet been made clear enough. The author feels that such relations must be clear before alder can be utilized as a forestry tree species.

In comparing the main ingredients of fresh leaves (Table 5) we see the nitrogen contents of alder are especially higher than those of the other needle-leaved and broad-leaved trees. The author believes that this high nitrogen content is related to breakdown of leaves as the prey of soil fauna and consequent acceleration of humification by microbial activity.

Accordingly, it is natural that considerable amounts of humus and nitrogen, originating from decomposition of alder leaves, will be accumulated in the original humus- and nitrogen-poor soil, in a short time. However, there remains some question since, despite the fact that original soil acidity is nearly neutral and exchangeable calcium content is increased by decomposition of leaves, the soil is gradually being acidified. The values for hydrolytic acidity are particularly increasing. It is presumed that such a phenomenon is due to the influence of humus material which is immediately supplied to the soil by rapid decomposition of alder leaves. It is well known that acidity increases as decomposition of fallen leaves progresses (Yamaya, 1962).

On the other hand, in opposition to the experimental results of alder leaf decomposition, amounts of humus, nitrogen, and exchangeable calcium of soils are lower under closing canopy of alder forest, and soil acidities are stronger than those values under other neighboring forests. This is explained as follows:

It is generally recognized that the nutrient cycle under natural forest is: supply of fallen leaves→release of nutrients by leaf decomposition→absorption of nutrients by plant roots. Since growth of alder is very rapid and its material production is great, it is clear that large amounts of nutrients are also absorbed from the soil. But, leaf decomposition of alder is very rapid, so substances are quickly returned to the soil. For this reason, the author believes that the rate of nutrient cycling under alder forest is faster than that in other forests. Generally, it is said that the more rapidly leaves are decomposed, the faster the rate of nutrient cycling and the lower the nutrient content of the soil (Kira, 1960).

Under the closing forest, the cycling of substances is seen; but in the pot experiment, it is not, because nutrients are supplied by leaf decomposition but not reabsorbed by roots. For this reason, it is clear that the behavior of substances in soils is different under closing forest than in the pot experiment.

Thus, the nutrient content of soils in alder forest is not necessarily high because of rapid nutrient cycling, but when alder are cut, a large quantity of nitrogen will be supplied to the soil.

Table 6 shows the nitrogen content and the cation exchange capacity of leaves and roots of alder, used in the experiment on leaf-decomposition. Nitrogen contents of leaves and root nodules are generally high. And, judging from the values for cation exchange capacity, it is presumed that, in general, roots absorb nutrients and root nodules store nitrogen. Accordingly, the author believes, as previously stated, the nitrogen relation is the most important aspect of alder as a soil-improving tree.

TABLE 5. Comparison of principal ingredients of fresh leaves of alder and the others

Tree species	District of sample	Month sampled	N	P_2O_5	K_2O	CaO
			----------Percent----------			
Alnus inokumae	Aomori	Sept.	3.51	0.57	0.87	1.80
Castanea crenata	Kitatama	Oct.	1.69	.22	1.14	1.29
Quercus serrata	Kitatama	Oct.	2.02	.27	.92	1.55
Quercus crispula	Kitatama	Oct.	2.19	.27	1.11	1.49
Cryptomeria japonica	Aomori	April	.79	.18	.95	.85
Pinus densiflora	Aomori	April	1.35	.17	.75	.24
Thujopsis dolabrata	Aomori	April	.73	.11	.72	1.94

Kitatama district (Nakatsuka, 1943).
Aomori district (Yamaya, 1962).

Conclusions

From the facts stated above, the following conclusions can be drawn.

1. Alder supplies a large quantity of carbon and nitrogen to the soil, but on the other hand, it clearly functions in acidifying the soil even while supplying considerable amounts of exchangeable calcium.

2. Since the rate of nutrient cycling under alder forests is very rapid, the nutrient contents of the soil are generally low. However, when the forest is cut and the nutrient cycle is broken, a large quantity of nitrogen is supplied to the soil.

It is necessary to know such features when planting alder or mixed stands of alder and other species, and also when turning cut-over areas to farmland.

TABLE 6. Comparison of cation-exchange capacity and nitrogen contents in leaves and roots of alder and Japanese cedar

Tree species	Part of tree	Cation-exchange capacity	Nitrogen
		Meq/100 g	*Percent*
	Leaves	55.58	3.24
Alder	Roots	179.75	1.06
	Root nodules	40.29	2.71
J. Cedar	Needle leaves	75.05	.86

Figure 4. Root nodules of alder.

Figure 5. Alder forest.

Acknowledgments

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Effect of organic matter and combined nitrogen on nodulation and nitrogen fixation in red alder[1]

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Abstract

Nodulation and growth in dry weight of red alder plants were influenced favorably by increasing levels of total soil nitrogen (TSN). Few but large nodules developed in soils with low TSN; in soils with high TSN, nodules were small but more numerous. Accretions of nitrogen to the systems and efficiency of nitrogen fixation peaked between 0.03 and 0.05 percent TSN. Nodulation was adversely affected by urea-nitrogen, but additions of 15-30 ppm of nitrate-nitrogen had a stimulating effect; at higher concentrations, even nitrate-nitrogen depressed the nodulation. Rates of nitrogen fixation of over 300 kg/ha year, determined under red alder stands 2-14 years old, were substantiated by greenhouse experiments. Based on efficiency of nitrogen fixation of about 5.4 mg N/day g nodule, dry weight, rate of fixation could reach 140 kg/ha year of nitrogen in a 7-year-old alder stand, and up to 209 kg/ha year in a 30-year-old stand. Based on average accretion of 220 mg of nitrogen per kilogram of soil, nitrogen fixation could approach 100 kg/ha during the first year in the field.

Introduction and Review of Literature

This paper summarizes results of three greenhouse experiments to investigate the effects of organic matter and of combined nitrogen on nodulation and nitrogen fixation of red alder (*Alnus rubra* Bong.). The objectives were to provide supporting evidence for nitrogen fixation by red alder and to determine rates of nitrogen fixation that are likely to occur in nature. Rates of nitrogen fixation were estimated from these experiments and compared with data obtained in the field.

Conclusive evidence for nitrogen fixation in alder (*A. Glutinosa* (L.) Gaertn.), both in vitro and in the field, was provided by Bond (1955 and 1956) who used N^{15} in his studies. He and his coworkers (Bond, Fletcher, and Ferguson, 1954) also studied the development of nodules in this species and concluded that nodules may appear 2-3 weeks after inoculation or sooner if the endophyte is present in soil when the seed germinates.

Various environmental factors such as soil pH, light, aeration, and combined nitrogen may influence both nodulation and nitrogen fixation (Bond, 1955; Bond et al., 1954; Daly, 1966; Ferguson and Bond, 1953; Stewart, 1962 and 1966; Stewart and Bond, 1961; Virtanen, 1957; Virtanen and Miettinen, 1963). Favorable effect of light and aeration on nodulation and nitrogen fixation is reported by various researchers (Bond et al., 1954; Ferguson and Bond, 1953; Quispel, 1958). Ammonium- and nitrate-nitrogen may influence nodulation and nitrogen fixation in various *Alnus* species. Bond and coworkers (1954) and Stewart and Bond (1961) observed that, after addition of 10-100 ppm of ammonium-nitrogen to the nutrient solution for experimental plants, nodule weight increased more than with control plants, but the number of nodules were fewer with 50 and 100 ppm of this form of combined nitrogen. Similar results were obtained by Quispel (1958) and by Daly (1966) when they added nitrate-nitrogen to their nutrient solutions.

Results of various greenhouse experiments indicate that *Alnus* species may fix nitrogen very efficiently. Ferguson and Bond (1953) have shown that the efficiency of nitrogen fixation of *A. glutinosa* plants may even surpass that of many legumes. The efficiency ranges from 0.4 to 16.3 mg of N/day g nodules in *A. glutinosa* (Stewart, 1962), and from 5.3 to 12.9 in *A. rugosa* (Du Roi) Spreng. (Daly, 1966); it is greatest in the young nodules of alder and other nonleguminous nitrogen fixers and decreases with age, presumably because of development of inactive tissues (Stewart, 1966). Conversely, Russell and Evans (1966) report that the efficiency of nitrogen fixation in *Ceanothus velutinus* var. *laevigatus* (Hook.) Torr. and Gray increases with age.

Virtanen (1957) and Virtanen and Miettinen (1963) report that *A. glutinosa* fixed about 40 grams of nitrogen per plant in 8 years, which corresponds to an annual rate of about 125 kg/ha for an alder thicket in the field. Crocker and Major (1955) estimated that the annual rate of nitrogen accretion under *A. sinuata* (Reg.) Rydb. growing in the areas of receding glaciers in Alaska reached about 62 kg/ha. For the same areas, Lawrence (1958) asserts that up to 155 kg/ha year of nitrogen may be fixed by a 5-year-old *A. sinuata* thicket. Accretions of this magnitude were determined by Daly (1966) under *A. rugosa* in Quebec; he calculated that from 155 to 165 kg/ha of nitrogen may be added annually to the soil by this shrubby species. According to Tarrant and Miller (1963) about 40 kg/ha year of nitrogen were added to the soil in a mixed plantation of red alder (*A. rubra* Bong.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), in Washington. Worthington, Ruth, and Matson (1962) estimated that about 62 kg/ha of nitrogen may accumulate annually in the ecosystem described by Tarrant and Miller (1963). These quantities are comparable to rates of nitrogen fixation determined for other such woody nonleguminous nitrogen fixers as *Casuarina equisetifolia* (Dommergues, 1963), *Hippophae rhamnoides* (Stewart, 1966), *Coriaria arborea* (Walker, 1964), and *Ceanothus velutinus* Dougl. (Wollum and Youngberg, 1965; Zavitkovski and Newton, 1967); but all these quantities are below the maxima reached by some legumes that fix up to 680 kg of nitrogen per hectare year (Sears et al., 1965).

Nitrogen accretions may occur from within the root zone of both nitrogen fixers and nonfixers. Nitrogen may be secreted in various forms from the roots and nodules and utilized by other plants (Virtanen, 1957; Virtanen and Miettinen, 1963). It seems likely, however, that most of the nitrogen added within the root zone is nitrogen fixed by free-living nitrogen-fixing micro-organisms. Nitrogen accretions of 73-90 kg/ha year are reported by Knowles (1965) and Parker (1957) for various soils of the temperate region. Much larger quantities of nitrogen may be fixed by such microflora in tropical rain forests: accretions ranging from 120 to 700 kg/ha year are reported by Jaiyebo and Moore (1963) for shrub communities that apparently contained no nitrogen-fixing plant species.

Materials and Methods

Greenhouse experiments. – Six levels of total soil nitrogen (TSN) – 0.011, 0.031, 0.052, 0.092, 0.183, and 0.504 percent – were achieved by adding pulverized Scotch broom litter to a nitrogen-deficient cinder soil. Groups of 10 quart-size cans were filled with each soil and several alder seeds planted in each. After germination, the plants were thinned to two per pot. These seedlings were inoculated with crushed nodules. They were kept in a greenhouse, watered well, and supplied regularly with a nitrogen-free nutrient solution. Effluents were collected and returned to the systems. After 180 days, half of the seedlings in each treatment (5 cans, 10 seedlings) were carefully removed and separated from the soil; both soil and plant material were dried at 70 C, and dry weights of plants, nodules, and soil were determined. The remaining seedlings were treated the same way when they reached 200 days of age. Total nitrogen (Kjeldahl method) was then determined for both plant material and soil. From these data a nitrogen balance sheet for each can was calculated.

In another greenhouse experiment, three 1-week-old red alder seedlings were planted in thirty-six 1-gallon pots filled with subsoils from three locations in Oregon: Coast Ranges, Metolius River, and junction of the Santiam highways in the Cascade Range. These soils contained, respectively, 0.02, 0.03, and 0.01 percent of TSN. They were designated as clayey, pumice, and cinder soils. To some pots, urea was added to produce levels of total soil nitrogen corresponding to 0.05, 0.1, and 0.2 percent. Nitrogen-free nutrient solution was added at regular intervals. Red alder seedlings were grown for 250 days in these soils; the seedlings and soils were treated as described above.

In a third greenhouse experiment, two 1-week-old red alder seedlings were planted in each of 33 pots in a sandy soil supplemented with 0, 15, 30, 60, 120, and 240 ppm of urea- or nitrate-nitrogen. These seedlings were grown for 160 days before dry weights of entire plants and of nodules in each can were determined.

Field studies. – The biomass approach described by Zavitkovski and Newton (1967) was used in estimating nitrogen fixation rates under field conditions. Nitrogen contents in soil, litter, and standing trees were determined

by obtaining dry weights per hectare and nitrogen percentages of these components. Thirty-six stands ranging from 2 to 61 years in age were sampled between 1964 and 1967. In two stands, quantities of nodules were determined by taking 50 soil cores to a depth of about 15 cm and screening out the roots and nodules.

Results

Greenhouse experiments. — Dry weights of red alder plants were increased by increasing levels of TSN. After an initial sharp increase, dry weights of these seedlings decreased at 0.09 percent TSN and increased again at even higher levels of TSN. Similar depressions in dry weights were observed in Scotch broom and snowbrush seedlings under identical conditions (Fig. 1). Depression was also noticeable in the generally ascending curves of nitrogen content (in mg) of red alder plants. The depression was of smaller magnitude because it was partially offset by increasing percentages of nitrogen in the plant material (Figs. 2 and 3). Nodulation showed a similar trend (Fig. 4).

Nodules formed clusters ranging in size from 2 to 15 mm. In general, few, large, pale-green and orange clusters located near the soil surface were found on roots of red alder plants in soils with low TSN nitrogen percentages; however, many, small, orange clusters distributed throughout the soil mass were more common in soils with high TSN. These characteristics may be
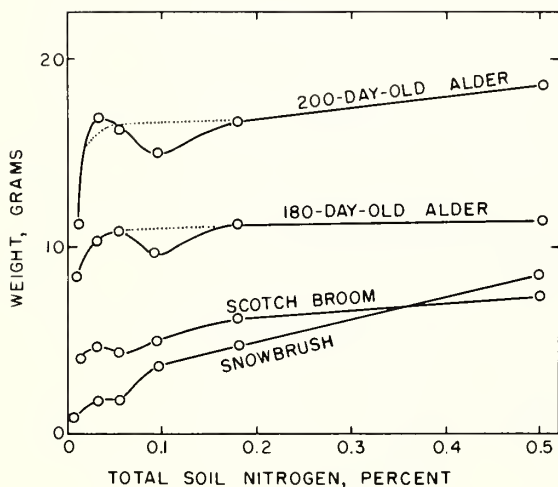
Figure 1. The effect of total soil nitrogen on average dry weight of red alder plants.
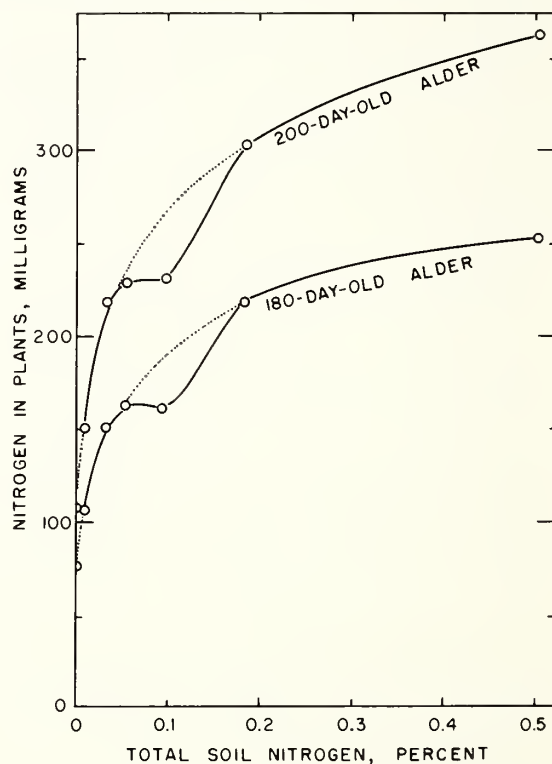
Figure 2. The effect of total soil nitrogen on weight of nitrogen in red alder plants.
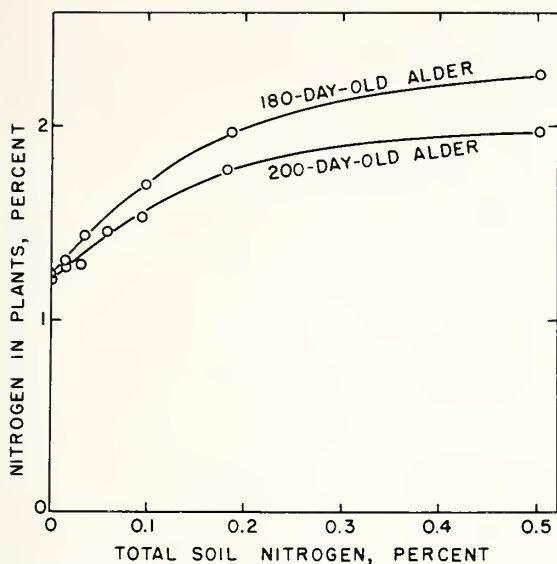
Figure 3. The effect of total soil nitrogen on percentage of nitrogen in red alder plants.
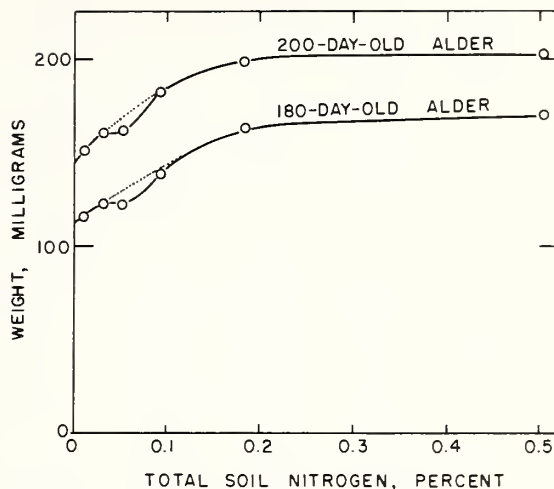
Figure 4. The effect of total soil nitrogen on average dry weight of nodules for each plant.

associated with the observed decrease in the efficiency of nitrogen fixation in soils with more than 0.2 percent TSN (Table 1).

The efficiency of nitrogen fixation was calculated from net accretions of nitrogen to the systems and expressed in mg of nitrogen fixed per day by one gram dry weight of nodule (Table 1). By extrapolating accretions of nitrogen (Fig. 5) and nitrogen in plants (Fig. 2) to zero of TSN it was possible to estimate the proportions of fixed and combined nitrogen in red alder seedlings at various levels of TSN (Fig. 6, Table 2). The results indicate

Figure 5.
Nitrogen accretion to the system at various levels of total soil nitrogen.

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TABLE 1. Efficiency of nitrogen fixation in red alder seedlings, by age

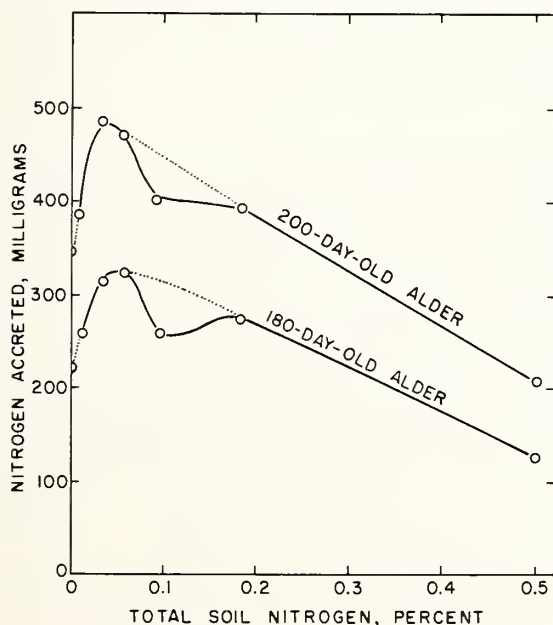| Soil	Total soil nitrogen	N added to systems			Dry weight of nodules			Nitrogen fixed[1]			
		180 days	200 days	250 days	180 days	200 days	250 days	180 days	200 days	Last 20 days	250 days
	Ppm	Mg	Mg	Mg	Mg	Mg	Mg	Mg	Mg	Mg	Mg
Cinder +	0[2]	220	340								
organic	110	256	386		231	305		6.15	6.34	21.3	
materials	312	316	489		247	321		7.10	7.61	26.9	
	518	322	472		243	324		7.37	7.29	23.2	
	921	259	400		279	365		5.16	5.48	19.3	
	1825	271	391		327	398		4.60	4.91	15.1	
	5040	127	205		340	406		2.08	2.53	9.9	
Clayey	200			510			645				3.16
Pumice	300			903			662				5.45
Cinder	110			771			594				5.21

[1] *Efficiency of nitrogen fixation in mg N/day g nodule, dry weight.*
[2] *Values of zero level obtained by extrapolation.*

that less than 20 percent of nitrogen in plants was contributed by fixation at the highest level of TSN used in this experiment. Although this represents a sharp drop from the proportion of fixed nitrogen at zero level of TSN (100 percent), the absolute rate of fixation was still almost 2/3 of nitrogen fixed at zero level TSN.

Nodulation was adversely affected by urea applied to three subsoils (Fig. 7). An addition of 200 ppm of urea-nitrogen reduced the dry weight of nodules from about 220 mg/plant to 50 mg/plant and to zero after 700 ppm
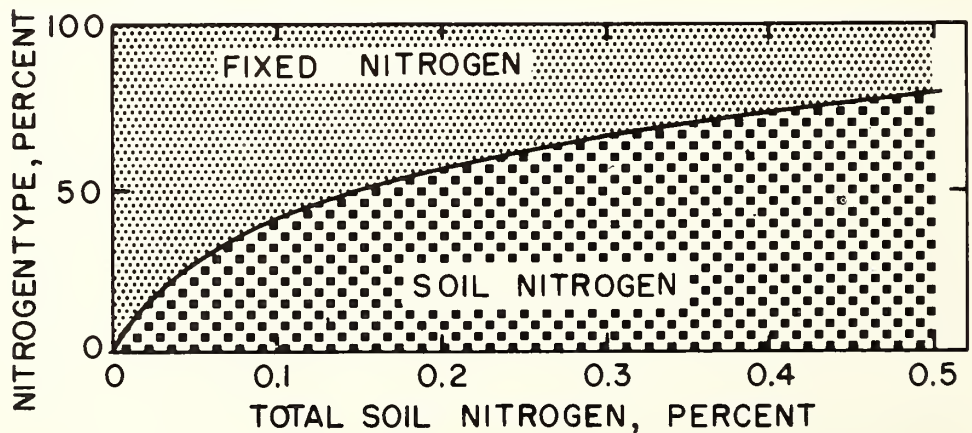

Figure 6. Percentages of fixed and combined nitrogen in plants at various levels of total soil nitrogen.

TABLE 2. Proportions of nitrogen fixed and combined nitrogen in red alder seedlings grown in soils supplemented with organic matter, by age

Accretion of N		Nitrogen in plants		Nitrogen in plants by fixation[1]				Nitrogen in plants from soil		Relative[2] magnitudes by fixation	
180 days	200 days	180 days	200 days	180 days		200 days		180 days	200 days	180 days	200 days
- - - - Mg - - - -		- - - Mg - - - -		Mg	Percent	Mg	Percent	- - - Percent - - -		- - - - Percent - - - -	
220[3]	340	158	228	158	100.0	228	100.0	0.0	0.0	100.0	100.0
256	386	216	300	184	85.2	259	86.5	14.8	13.5	116.5	113.5
316	489	300	437	227	75.7	328	75.1	24.3	24.9	144.0	144.0
321	472	322	457	231	71.9	316	69.2	28.1	30.8	146.0	139.0
259	400	319	460	186	58.3	268	58.3	41.7	41.7	118.0	117.5
271	391	439	604	195	44.5	262	43.3	55.5	56.7	123.5	115.0
127	205	510	724	91	17.8	137	18.9	82.2	81.1	57.5	60.2

[1] Values of nitrogen in plants by fixation are based on values at zero level using the following formula:

$$\frac{N \text{ in plants at zero level TSN} \times 100}{\text{Net N accretion at zero level TSN}}$$

The corresponding percentages for seedlings 180 and 200 days old are 72 and 67 percent. The proportions of N by fixation in plants were determined by multiplying the values of net N accretions at the particular levels of TSN by 0.72 or 0.67.

[2] Relative magnitudes compare amounts of nitrogen in plants by fixation among themselves.

[3] Values of zero level obtained by extrapolation. See Figures 2 and 5.

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of urea-nitrogen was added. All three soils were similar in this respect. Compared to sandy soil, these subsoils had higher buffering capacity. In sandy soil, nodulation was reduced to half by an addition of 60 ppm of urea-nitrogen and to 10 percent at 120 ppm; complete suppression of nodulation occurred at 240 ppm of urea-nitrogen. Nodulation was less affected by the same levels of nitrate-nitrogen; it was actually stimulated by additions of 15 and 30 ppm of nitrate-nitrogen; with 60 ppm it still remained high at 70 percent, while the corresponding values for 120 and 240 ppm of nitrate-nitrogen were about 20 and 10 percent (Fig. 8).

Dry weights of red alder plants were also adversely affected by additions of urea (Fig. 9). An addition of 300 ppm of urea-nitrogen to the clayey soil slightly increased dry weights of the alder, but 200 and 400 ppm reduced dry weights in cinder and pumice soils. At higher concentrations, the growth was suppressed substantially, and the shape of the curves suggests that all seedlings would be killed by additions of over 1,100 ppm of urea-nitrogen in cinder and pumice soils. Much higher concentrations would be needed for killing alder plants in the clayey soil. In the sandy soil, additions of 15 and 30 ppm of either urea- or nitrate-nitrogen stimulated the growth in dry weight, but at higher concentrations the growth was depressed (Fig. 10). Again urea-nitrogen had a more depressing effect than nitrate-nitrogen.

Percentages of nitrogen in plant material showed no change upon addition of 200 to 400 ppm of urea-nitrogen to three subsoils, but at higher concentrations, percentages increased sharply. A maximum of over 5 percent of nitrogen was found in two tiny red alder seedlings growing in clayey soil supplemented with 1,800 ppm of urea-nitrogen (Fig. 11).

Nitrogen fixation expressed in mg of nitrogen fixed per kg of soil showed a decreasing trend with increasing levels of added urea-nitrogen (Fig. 12). This depression was less pronounced in the clayey soil than in pumice and cinder soils. On the average, 220 mg of nitrogen per kg of soil were added in 250 days under very favorable environmental conditions (of temperature and moisture) in a greenhouse.
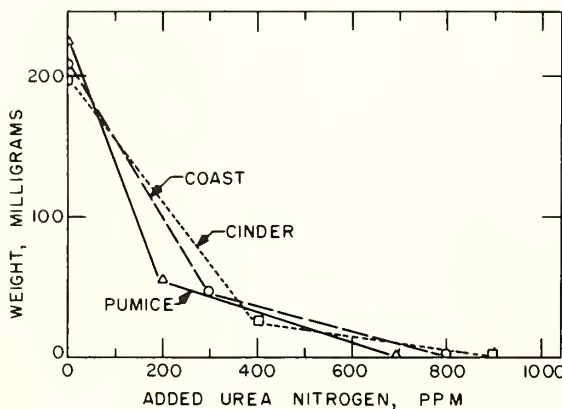
Figure 7.   The effect of urea on average weight of nodules for each red alder.
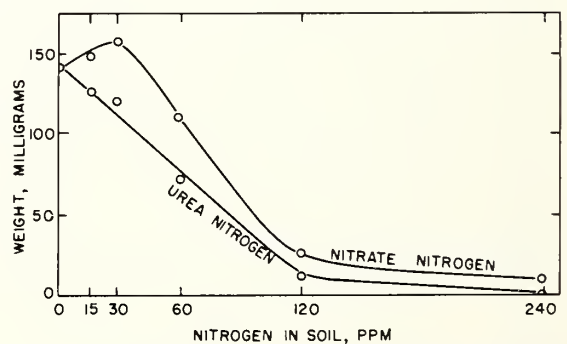
Figure 8.   The effect of combined nitrogen on average dry weight of nodules for each red alder.

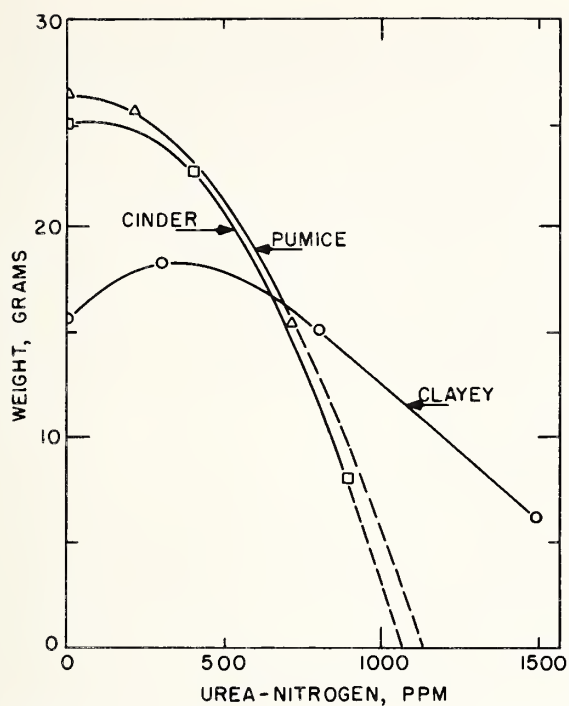Figure 9. The effect of added urea-nitrogen on average growth in dry weight of each red alder.
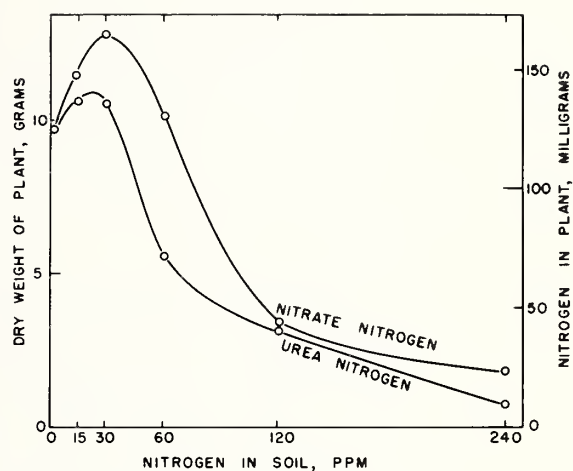

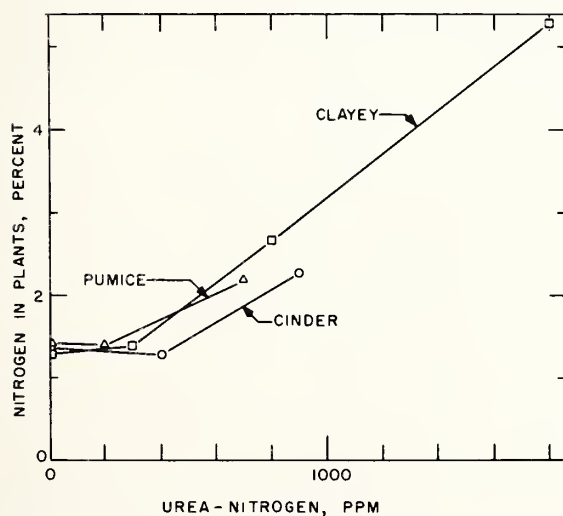Figure 10. The effect of combined nitrogen on average growth and nitrogen content of red alder.

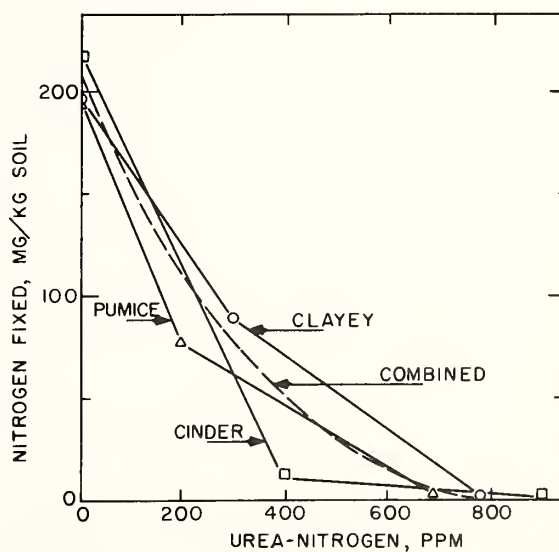Figure 11. The effect of added urea-nitrogen on nitrogen content of red alder seedlings.

Figure 12. The effect of urea-nitrogen on nitrogen fixation in red alder.

Field studies. — Biomass study and analyses of soils revealed that over 300 kg/ha year of nitrogen may be added to the ecosystems dominated by red alder, between the ages of 2 and 14 years. Most of this nitrogen is incorporated rapidly into the soils; only about 20 percent is tied up in the biomass. Annual litter fall contributes about 100 kg/ha of nitrogen to the soil while 35 kg/ha more is incorporated in the above-ground parts of the stands.

The amounts of nodules were determined in only two stands. In a 7-year-old fully stocked stand, an equivalent of 87.6 kg/ha of nodules was found; in a 30-year-old stand, 183 kg/ha. Both values include only nodules in the upper 15 cm of the soil profile. An estimated additional 30 percent or more may exist in layers below the 15 cm depth, for a total of about 117 and 244 kg/ha of nodules in these two stands.

Discussion

Extrapolating results obtained under greenhouse conditions into the field may lead to erroneous conclusions unless some basis for this procedure is established in nature. In this study such a basis has been established tentatively and the integration of the results obtained in the greenhouse with those in the field is believed to make possible reasonable field estimates. In using the greenhouse experiments, more credit has been given to the results obtained in soils supplemented with organic matter, since this seemed to represent field conditions more closely than those with inorganic supplements. Levels of combined nitrogen used in these greenhouse experiments could seldom be reached in nature; the highest concentrations could occur only within restricted microsites after heavy applications of nitrogen fertilizers. In view of this, the depressions of nodulation, of dry weight production, and of nitrogen fixation by combined nitrogen are more of academic than of practical significance, especially since nodulation was not prevented even in soils with the highest amounts of organic matter (0.5 percent TSN), and since similar observations were made in the field where large masses of nodules are commonly found in upper soil horizons that are very rich in organic matter.

Presence of nodules is generally considered prima facie evidence for nitrogen fixation. The present study provides supporting evidence, although morphology of nodules may influence capacity for fixation. There is also evidence that the efficiency of nitrogen fixation in nodulated red alder seedlings may be affected by high levels of decomposing organic matter. It was not possible to establish the nature of this depression. One reason could be that red alder plants will utilize combined nitrogen in preference to fixed nitrogen, possibly because of relative energy demand for utilizing nitrogen from various sources. This reasoning finds support in the apparently preferential utilization of combined nitrogen in soils supplemented by either urea- or nitrate-nitrogen observed in this study and also reported by Stewart and Bond (1961) for *A. glutinosa* and by Daly (1966) for *A. rugosa*. In these studies, however, the absolute amounts of nitrogen fixed or the efficiency of nitrogen fixation remained steady over a range of concentration of combined nitrogen. It seems, therefore, that combined nitrogen alone is not responsible

for the reduction of nitrogen fixation in soils with high contents of organic matter. No study with woody nitrogen-fixers is known to us that would describe the effect of organic matter on nitrogen fixation. In some legumes, however, return of clippings to the soil reduced nitrogen fixation by almost 50 percent (Sears et al., 1965). Inhibition of nodulation, and presumably of nitrogen fixation, by high levels of organic matter was reported by Zavit-kovski and Newton (1967) in snowbrush.

Net accretions of nitrogen to the systems may be explained in terms of nitrogen fixation by red alder and by free-living nitrogen-fixing micro-organisms. By extrapolating these nitrogen accretions (Fig. 5) and nitrogen in plants (Fig. 2) to zero (zero percent of TSN) the proportions of nitrogen fixed by each of these two mechanisms were tentatively estimated at 72 percent and 28 percent by red alder and microflora, respectively, for 180-day-old plants, and at 67 percent and 33 percent for 200-day-old plants. (Note that nitrogen accretions in Fig. 5 refer to two plants growing in one pot.) These proportions were used for calculations in all six treatments (Table 2). When we compare amounts of nitrogen added to the systems with those tied up in the plants, it becomes apparent that, theoretically, in soils with more than 0.05 percent TSN all nitrogen added to these systems could be tied up in the plant material (Table 3). This means that the organic matter may have some adverse effect only on nitrogen fixation by free-living micro-organisms. However, it seems more reasonable to assume that both processes are affected at the same time and to the same degree. In Table 3 higher percentages of nitrogen accretions may be noted in the 200-day-old plants, which seems to indicate that the proportion of nitrogen fixed by microflora or released directly to the soil is increasing with age.

Results of the field study indicate that more nitrogen is added to the soil from within the soil (about 60 percent) than indirectly from litter fall (40

TABLE 3. Comparison of nitrogen accretions with nitrogen tied up in red alder plants, by age

Soil	Total soil nitrogen	Nitrogen in plants		Nitrogen accretion		Nitrogen added[1]	
		180 days	200 days	180 days	200 days	180 days	200 days
	Percent	*- - - - Mg - - - -*		*- - - - Mg - - - -*		*- - - Percent - - -*	
Cinder +	0.000[2]	158	228	220	340	139.0	149.0
organic	0.011	216	300	256	386	118.5	128.5
materials	0.031	301	437	316	489	105.5	112.0
	0.052	322	457	321	472	100.0	103.5
	0.092	319	460	259	400	81.0	87.0
	0.183	439	604	271	391	61.5	64.5
	0.504	510	724	127	205	25.0	28.5

[1] *Nitrogen accretion as percent of nitrogen in plants.*
[2] *Values of zero level obtained by extrapolation.*

percent). Accumulation of litter in 2- to 14-year-old red alder stands suggests that up to 5,000 kg/ha of litter may fall annually, and about 100 kg/ha of nitrogen may be added to the soils. This quantity apparently remains stable once the full occupancy of the site is reached, sometime during the second year after alder establishment. Only about 35 kg/ha of nitrogen are tied up in the aboveground parts each year. These two components account for 40 percent of the nitrogen added to the ecosystems. The origin of the remaining 60 percent of the total accretion is difficult to establish but probably involves secretions of nitrogen from nodules and roots into the soil and nitrogen fixation by free-living microorganisms. The existence of these two mechanisms can be shown by comparing the soil nitrogen percentages at the beginning of the greenhouse experiments with those at the conclusion (Table 4). The increase is highest in soils with low contents of organic matter, but accretions are decreasing with increasing TSN. The absolute increase does not change substantially, although it seems to be slightly greater at levels of TSN that are commonly encountered in the field (0.05 to 0.1 percent TSN) than at higher and lower levels.

Rates of nitrogen fixation determined in the field study are higher than values reported for various alder species (Crocker and Major, 1955; Daly, 1966; Lawrence, 1958; Tarrant and Miller, 1963; Virtanen, 1957; Virtanen and Miettinen, 1963; and Worthington et al., 1962) and for other nitrogen-fixing plants (Dommergues, 1963; Stewart, 1966; Walker, 1964; Wollum and Youngberg, 1965; and Zavitkovski and Newton 1967). Over 300 kg/ha year of nitrogen may be added to the ecosystems dominated by red alder between the ages of 2 and 14 years. Indirect evidence in support of this high rate of nitrogen fixation was provided by the greenhouse experiments. Efficiency of nitrogen fixation was calculated for both 180- and 200-day-old plants (Table

TABLE 4. Percentages of total soil nitrogen at the beginning and at the various conclusions of the experiments

Soil	Initial total soil nitrogen	Final total soil nitrogen			Increase			Absolute increase		
		180 days	200 days	250 days	180 days	200 days	250 days	180 days	200 days	250 days
	Ppm	- - - - - - - *Ppm* - - - - - - -			- - - - - *Percent* - - - - -			- - - - - *Ppm* - - - - -		
Cinder +	110	180	256		63.5	133.0		70	146	
organic	312	396	468		27.0	50.0		84	156	
materials	518	620	684		19.5	32.0		102	166	
	921	1046	1026		13.5	11.5		125	105	
	1825	1920	1935		5.2	6.0		95	110	
	5040	5020	5070		- .4	.6		- 20	30	
Clayey	200			230			15.0			30
Pumice	300			343			14.5			43
Cinder	110			150			36.5			40

1). When these values are used, potential rates of nitrogen fixation in the field could be approximated from known weight of nodules in a red alder stand. In the 7-year-old stand with 117 kg/ha of nodules and fixation efficiency of about 5.4 mg of nitrogen per day per gram nodule weight (for soil with 0.11 percent TSN) about 140 kg/ha year of nitrogen may be fixed, assuming that in the coastal areas environmental conditions favorable for nitrogen fixation may be as long as 220 days per year. In the 30-year-old stand with 244 kg/ha of nodules and efficiency of about 3.9 (for soil with 0.31 percent TSN) the fixation could reach 209 kg/ha year. Nitrogen fixation rates of a similar magnitude could also be calculated from the greenhouse experiment with three subsoils. In control pots, 220 mg of nitrogen per kilogram of soil were added in 250 days under generally favorable greenhouse conditions. Average bulk density of these soils is close to 1.0, hence 2,000,000 kg/ha of soil may be present in the upper 20 cm layer. Without any correction for differences in the environment and for the length of growing season, some 440 kg/ha year of nitrogen could be fixed. Note, however, that tops of the red alder seedlings in the greenhouse occupied an area 2-3 times larger than the area of the pot. Adjusting for all these factors, a reasonable estimate of nitrogen fixation for the first year of growth would approach 100 kg/ha.

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Red alder deficiency symptoms and fertilizer trials[1]

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Introduction

Recent studies of *Alnus rubra* Bong. have demonstrated that it plays a valuable role in increasing the nitrogen status of soils. There is good evidence (Tarrant and Miller, 1963; Franklin et al., 1968) that red alder nodules fix atmospheric nitrogen, as do the nodules of European *Alnus* species (Rodriguez-Barrueco and Bond, 1968). Studies of other alder species have demonstrated some elemental requirements for the development of nodules but, as with red alder, requirements for growth of the trees have received little attention.

In this study emphasis was placed on developing visual deficiency symptoms and chemical guidelines for use in diagnosing deficiencies of nitrogen, phosphorus, potassium, calcium, and magnesium in red alder seedlings. A concurrent pot culture study was conducted with seedlings grown in pots of Lynden loam soil. Amendments of nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur were applied in an additive method. Growth responses were evaluated using the guidelines developed in the deficiency development study. The nutrient status of seedlings grown in the field on the Lynden loam soil was compared to that of unfertilized seedlings in the pot culture study so as to provide a basis for interpreting the potential applicability of these results to the field.

Methods

All seed used in this investigation was obtained from a single 50-year-old red alder, growing on an Alderwood soil just south of Seattle, Washington. Seed was collected in October of 1965 and held in cold storage. Seedlings were grown in flats of silica sand until two true leaves developed. Crushed nodule solution was applied to all root systems as seedlings were transplanted.

For the development of deficiencies, seedlings were transplanted into 3-gallon crocks filled with silica sand. Five seedlings were planted in each crock on May 1, 1966. Duplicates were prepared for each treatment, except for three sets in the case of the "complete". Treatments were "complete", and 1/20 and 1/100 of this full nutrient level for nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur respectively. The "complete" solution was modified from Hoagland and Arnon (1938) by Walker, Gessel,

and Haddock (1955). Composition of the solutions are presented in Table 1. After 10 weeks the 1/20 levels of phosphorus, calcium, and sulfur were reduced to 1/1000 with the intention of developing visual deficiency symptoms since none had appeared at the 1/100 levels. Solutions were pumped from carboys into the crocks four times a day by means of a timed air pressure system. Seedling heights were measured every 2 weeks. All treatments were harvested after 14 weeks.

Lynden loam soil for the fertilizer trials was collected from a red alder study area on the Pilchuck Tree Farm near Arlington, Washington. The top 6 inches of the mineral soil was collected, air-dried, and sieved through a ¼-inch mesh screen. The plants were grown in 6-inch plastic pots, with glass plates placed over the holes at the bottoms of the pots to permit drainage. Fourteen hundred grams of soil were placed in each pot, after appropriate

TABLE 1. Solutions used in red alder seedling deficiency development study [1]

Compound	"Complete"	N 1/20	P 1/20	K 1/20	Ca 1/20	Mg 1/20	S 1/20
NH_4H_2PO4	0.50	0.025	0.025	0.50	0.50	0.50	0.50
KNO_3	3.00	--	3.000	.15	3.00	3.00	3.00
$Ca(NO_3)_2$	2.00	.175	2.000	2.00	.10	2.00	2.00
$MgSO4$	1.00	1.000	1.000	1.00	1.00	.05	.05
NaH_2PO4	--	.475	--	--	--	--	--
KCl	--	3.000	--	--	--	--	--
$CaCl_2$	--	1.825	--	--	--	--	--
$NH4Cl$	--	--	.475	--	--	--	--
$NaNO_3$	--	--	--	2.85	3.80	--	--
Na_2SO4	--	--	--	--	--	.95	--
$MgCl_2$	--	--	--	--	--	--	.95
ppm N	105.0	5.2					
P	15.5		.78				
K	117.0			5.9			
Ca	80.0				4.0		
Mg	24.0					1.2	
S	32.0						1.6

Micronutrient concentrations in ppm of the element were:

Fe (as NaFe EDTA)	5.00 ppm	Cu (as $CuCl_2$ +$2H_2$0)	0.020 ppm
B (as H_3BO_3)	0.50 ppm	Zn (as $ZnCl_2$)	0.050 ppm
Mn (as $MnCl_2$ +$4H_2$0)	0.50 ppm	Mo (as Na_2Mo04+$2H_2$0)	0.050 ppm

[1] Solutions modified from Hoagland and Arnon (1938) by Walker, Gessel, and Haddock (1955).
[2] Same compounds were used in 1/100 and 1/1000 solutions with similar reciprocal substitutions.

fertilizers had been mixed with the soil, following a method similar to that of Jenny et al. (1950). Amounts of fertilizers and compounds used are presented in Table 2. Three inoculated seedlings were transplanted into each pot on May 1, 1966. The pots were placed in shallow Pyrex dishes; four replicates of each treatment were prepared.

The potted seedlings were watered two to three times per week. After 10 weeks, seedlings in all treatments were growing poorly and it was thought that restricted aeration and drainage may have been contributing factors. At this time glass plates inside the pots were removed in all treatments, as were the Pyrex dishes supporting the pots. Growth of seedlings in all treatments improved after these measures were taken. All treatments were harvested after 20 weeks.

All seedlings in both the deficiency development study and the pot culture study were separated into roots, leaves, stems and nodules at harvest. Ovendry weights (70 C) were obtained for each component of each seedling. For analyses, foliage from the seedlings in each crock was combined. In addition, in the low nitrogen treatments, foliage of nodulated seedlings was separated from that of unnodulated seedlings. For the fertilizer study, all leaf tissue from a treatment was combined. Leaf tissue was collected from 1- and 2-year-old red alder seedlings growing in the field at the site where the soil for the pot tests was collected.

Digestion of leaf tissue was accomplished with sulfuric acid and hydrogen peroxide as described by Naponen et al. (1947). Nitrogen was determined using a micro-Kjeldahl distillation apparatus. Phosphorus was determined

TABLE 2. Compositions of fertilizers used in pot culture study with red alder seedlings[1]

Treatment	Milligrams of fertilizer per 1,400 grams of soil (per pot)					
	NH_4NO_3	NaH_2PO_4	K_2SO_4	$CaCO_3$	Na_2SO_4	$MgCl_2$
N_3[2]	600					
$P_{3.5}$		474				
$N_3 P_{3.5}$	600	474				
$N_3 P_{3.5} S$	600	474			207	
$N_3 P_{3.5} K_2 S$	600	474	259			
$N_3 P_{3.5} K_2 SCa$	600	474	259	2800		
$N_3 P_{3.5} K_2 SCaMg$	600	474	259	2800		83

N_3 = 300 pounds per acre N   S = 68 pounds per acre S

$P_{3.5}$ = 350 pounds per acre P_2O_5 Ca = 4,000 pounds per acre $CaCO_3$

K_2 = 200 pounds per acre K_2O Mg = 30 pounds per acre Mg

[1]Method of additions modified from Jenny et al. (1950).
[2]After 11 weeks an additional 300 pounds per acre of nitrogen was added to each treatment containing nitrogen fertilizer.
Conversion factor: 1 pound per acre = 0.5 part per million.

colorimetrically using the vanadomolybdate method described by Jackson (1964). Potassium was determined by flame spectrophotometry as described by Jackson (1964). Magnesium, calcium, manganese, and iron were determined using an atomic absorption spectrophotometer. Soil and solution pHs were measured with a glass electrode pH meter. In the case of soil pH, the "water saturation percentage" method was employed as described by Jackson (1964).

Results and Discussions

Deficiency Development Study

Nitrogen

The pale green foliage, slender reddish stems, and stunted growth developed in the low nitrogen treatments were typical of nitrogen deficiency. Growth was significantly reduced, at the 1-percent confidence level (Table 3). With the development of nodules in some seedlings in the low nitrogen treatments growth increased dramatically. Foliage of nodulated seedlings assumed normal size and the chlorotic appearance disappeared. Total nitrogen in the foliage increased to levels which would not indicate a nitrogen deficiency, although it is uncertain whether or not the deficiency was completely removed. In one replicate of the N 1/100 treatment 81 percent of the total yield of five seedlings was contained in the one well nodulated plant.

Bond and Hewitt (1962) concluded that cobalt is required for nitrogen fixation by *Alnus glutinosa* root nodules. Seedlings grown without cobalt developed acute chlorosis, characteristic of nitrogen deficiency. Although cobalt was not added to the nutrient solutions in the present study, fixation of nitrogen in nodulated seedlings in low nitrogen treatments appeared to be good as indicated in the above paragraph. Trace amounts of cobalt probably existed in the unpurified sand-solution system.

N level was not extremely low even in chlorotic seedlings, the lowest value being 2.36 (Table 2) for the 1/100 N treatment. Most other treatments showed over 3 percent N, but the 1/100 Ca plants had only 2.69 percent, although they were a normal green. This near overlapping of N values for chlorotic and green plants makes the recognition of N deficiency by chemical analysis certain only if the values are quite low, perhaps under 2.4 percent.

Analysis of nodule formation in the various treatments showed that nodulation was more frequent (40 versus 8 percent) and nodules were larger (averaging 0.12 versus 0.03 grams) in low nitrogen treatments than in other treatments. With adequate supplies of nitrogen, nodulation was retarded. A preliminary study showed similar results.

Phosphorus

Although significantly reduced growth was associated with the 1/100 level of phosphorus, no visual deficiency symptoms were evident. Foliar phosphorus content in the P 1/20 (changed to 1/1000) treatment was less than in the P 1/100 treatment but still no visual symptoms were evident. These findings indicate that growth of red alder may be seriously retarded without

TABLE 3. Summary of chemical analyses of red alder seedling leaf tissue from deficiency development study in a sand medium

Treatment		Yield[1]	N	P	K	Ca	Mg	Mn	Fe
		Grams				*Percent*			
"Complete"	A[2]	93.64	3.25	0.219	1.924	0.979	0.341	0.013	0.013
	B	68.84	3.43	.241	1.962	1.003	.366	- -	.011
	Average	81.24	3.34	.230	1.943	0.991	.353	- -	.012
N 1/20	A	11.75	2.72	.317	- -	- -	- -	- -	- -
without	B	8.65	2.47	.291	- -	- -	- -	- -	.016
nodules	Average	10.20	2.59	.304	- -	- -	- -	- -	- -
N 1/100	A	3.68	2.36	.307	3.153	1.320	.353	-	.026
	B	1.95	2.36	.304	3.277	1.152	.325	.025	.043
	Average	2.81	2.36	.306	3.206	1.236	.339	- -	.035
N 1/20	A	33.05	3.15	.297	- -	- -	- -	- -	.046
with	B	22.65	3.05	.298	- -	- -	- -	.033	.019
nodules	Average	27.85	3.10	.297	- -	- -	- -	- -	.033
N 1/100	A	26.45	3.34	.315	2.325	1.042	.360	.028	.017
nodules	B	20.85	3.25	.292	2.350	.677	.360	.033	.035
	Average	23.65	3.29	.304	2.375	.860	.360	.030	.026
P 1/20	A	65.64	2.95	.080	- -	- -	- -	.021	.013
(1/1000)	B	47.68	3.18	.092	- -	- -	- -	.025	.012
	Average	56.66	3.07	.086	- -	- -	- -	.023	.012
P 1/100	A	26.27	3.27	.152	1.887	.521	.419	.035	- -
	B	31.22	3.26	.116	1.825	.840	.400	- -	.053
	Average	28.74	3.27	.134	1.856	.680	.409	- -	- -
K 1/20	A	80.29	3.20	- -	.488	- -	- -	.015	.010
	B	44.71	3.06	- -	.452	- -	- -	.019	- -
	Average	62.50	3.13	- -	.470	- -	- -	.017	- -
K 1/100	A	27.89	3.45	.549	.361	1.278	.608	.030	- -
	B	44.90	3.30	.440	.373	1.394	.560	.034	- -
	Average	36.39	3.38	.495	.367	1.336	.584	.032	- -
Ca 1/20	A	105.03	- -	- -	- -	.077	- -	- -	- -
	B	47.02	- -	- -	- -	.077	- -	- -	- -
	Average	76.02	- -	- -	- -	.077	- -	- -	- -
Ca 1/100	A	81.25	2.69	.207	2.244	.151	.374	.018	.015
	B	38.78	2.64	.201	1.975	.168	.424	- -	- -
	Average	60.01	2.66	.204	2.109	.160	.399	- -	- -
Mg 1/20	A	61.76	3.14	- -	- -	- -	.110	- -	- -
	B	52.59	3.33	- -	- -	- -	.108	- -	- -
	Average	57.17	3.24	- -	- -	- -	.109	- -	- -
Mg 1/100	A	50.40	3.26	.315	2.662	.987	.089	- -	- -
	B	39.64	3.36	.320	2.675	.997	.088	.032	.016
	Average	45.07	3.31	.318	2.669	.987	.088	.032	- -

[1] Total ovendry weight of seedlings per crock.
[2] "A" and "B" are separate crocks (duplicates) of the same treatment.
Note: Yields indicated in N 1/20 and N 1/100 treatments which were separated into those with and without nodules, are extrapolated to represent five seedlings per crock.
Dashed lines indicate that no determination was made.

the appearance of any visual symptoms. Foliar phosphorus levels less than 0.16 percent were associated with reduced growth and thus indicate a phosphorus deficiency.

Potassium

"Scorched" margins of some leaves characterized potassium deficient foliage. Deficiency was noted in the K 1/100 but not the K 1/20 treatment. After 8 weeks, margins of older leaves appeared chlorotic. After 11 weeks, the margins were bright orange. Meyer and Anderson (1939) recognized marginal "scorching" to be a common potassium deficiency symptom. The K 1/100 treatment developed both diagnostic visual deficiency symptoms and showed significantly reduced growth; however, K 1/20 seedlings did not appear deficient by either criterion. This would indicate that visual symptoms are good indicators of potassium deficiency. Although growth was much less in the K 1/100 than the K 1/20 treatment, the foliar percentage of potassium was only slightly less (0.37 versus 0.47 percent) and thus a critical concentration is indicated at about 0.4 percent potassium. Foliar potassium levels in both the K 1/20 and K 1/100 treatments were far below the potassium contents of leaves from the "complete" (1.94 percent). This indicates that potassium contents are sensitive indicators of deficiency. Unusually high amounts of phosphorus and magnesium were found as well in foliage with low potassium. These patterns may also be characteristic of potassium-deficient foliage.

Magnesium

Foliage of the magnesium-deficient red alder seedlings developed gray or brown spotting along the leaf margins. This discoloration spread through interveinal areas, abscission typically occurring while areas adjacent to the veins were still green. Older foliage was affected first. About 46 percent of the total foliage produced in the Mg 1/100 treatment abscissed during the study, while 22 percent of the Mg 1/20 foliage abscissed. Abscission of "complete" foliage was only 3 percent. The stems of seedlings in the low magnesium treatment looked conspicuously bare. These foliar magnesium deficiency symptoms agree with those Meyer and Anderson (1939) describe as being typical. Ingestad (1962) noted similar magnesium deficiency symptoms in birch seedlings, except that areas along veins were not green when abscission occurred. The gray or brown spotting developing at the margins spread over the entire leaf blades in the birch.

Despite the appearance of visual deficiency symptoms in the Mg 1/20 treatment, yield was not significantly reduced if abscissed leaves were included. Walker, Gessel, and Haddock (1955) obtained similar results in a study with western redcedar seedlings. Growth restriction of red alder seedlings caused by magnesium should be detectable from associated visual symptoms.

Foliar percentages of magnesium correlating with deficiency were 0.11 percent for the Mg 1/20 treatment and 0.09 percent for the Mg 1/100 treatment. These are considerably below the magnesium contents of the "complete" (0.35 percent) or other treatments, indicating that magnesium

level may be a sensitive indicator of magnesium deficiency. Relatively high levels of phosphorus and potassium also characterized magnesium-deficient foliage.

Calcium

Diagnostic symptoms of calcium deficiency could not be induced despite the fact that foliar concentrations of calcium in the Ca 1/20 (changed to 1/1000) treatment were only 0.08 percent, as compared to 0.99 percent in the "complete" treatment. The statistical difference in the heights between Ca 1/1000 and "complete" treatments was largely due to stunted growth in one replicate. Seedlings in this crock were shaded more severely than in most other replicates and low calcium supply was not entirely responsible for the reduced heights. Other statistical criteria indicated no significant differences between Ca 1/100 and "complete" treatments with respect to dry matter production of stems, roots, and leaves. Biweekly height measurements did indicate a sharp decrease in height growth of Ca 1/20 (1/1000) seedlings in the final 2 weeks of the study. No diagnostic visual symptoms appeared, however. The foliar percentage of calcium in these seedlings was 0.08, which would appear to be at or near the critical Ca level for growth of red alder seedlings.

Sulfur

No deficiency symptoms were developed for sulfur and yield was not significantly affected by either low sulfur treatment in the 14 weeks of this study. Sulfur deficiencies might possibly have developed with a longer growth period.

Yield of S 1/100 treatment seedlings was greater than "complete" treatment seedlings, although this was not significant. Chemical analysis of these seedlings was not made. A summary of foliar content and deficiency symptoms for all elements used in this study is given in Table 4.

Pot Culture Study

The pot culture experiment developed limitations because of the problem with drainage and aeration (see methods), and is reported here only because of the information revealed regarding N and P responses, nodulation, and Mn toxicity. The results are believed to have little immediate application to the field, however.

Unfertilized red alder seedlings grown in pots of Lynden loam soil were found to be deficient in nitrogen and phosphorus, based on the guidelines which were developed. The seedlings also were presumed to be suffering from manganese toxicity since the foliage contained 0.95 percent manganese. The nutrient status of these seedlings was in sharp contrast to that of unfertilized seedlings grown on the Lynden loam soil in the field (Table 5). Seedlings grown in the field showed no evidence of nitrogen or phosphorus deficiency, nor of manganese toxicity. Nodules of pot culture seedlings did not fix sufficient nitrogen to relieve foliar chlorosis, in contrast to seedlings grown in the field on the Lynden loam soil. The phosphorus deficiency in

TABLE 4. Deficiency guidelines for red alder seedlings as observed in a sand medium

Deficient element	Foliar percentage corresponding with deficiency[1]	Effect on growth in study	Visual symptoms of deficiency
Nitrogen	2.4[2]	Stem height and weight, weight of roots and foliage significantly reduced	Small, pale green foliage Stems slender and reddish Roots small and thin
Phosphorus	.16	Stem height and weight, weight of roots and foliage significantly reduced	No specific symptoms
Potassium	.4	Stem height and weight, weight of roots and foliage significantly reduced	Margins of foliage chlorotic, later turning bright orange — "scorched." Older foliage affected first.
Calcium	.08	Stem height growth reduced	No specific symptoms
Magnesium	.11	Weight of foliage significantly reduced only because of abscissed foliage	Gray or brown spotting along leaf margins, spreading inward through interveinal areas. Abscission typically occurring while areas adjacent to veins still green. Older foliage affected first. Large amounts of abscissed foliage.

[1] *Guideline values.*
[2] *Below this value nitrogen deficiency is very likely. Strong nitrogen deficiency was found at 2.7 percent, however, so nitrogen deficiencies at higher values are possible.*

unfertilized pot culture seedlings, indicated by a 0.13 percent concentration in the foliage, may have developed after roots reached the bottoms of the pots and were thus restricted. This is suggested by the sharply reduced growth rate after 16 weeks in treatments containing the larger seedlings. Roots of larger seedlings were found matted along the bottom of pots when the seedlings were harvested, after 20 weeks of growth. It is also possible that unfertilized pot culture seedlings were deficient in phosphorus through-

TABLE 5. Comparison of nitrogen, phosphorus, potassium, calcium, magnesium, manganese, and iron in red alder seedlings in Lynden loam soil in the field and pot culture study, with the deficiency guideline values

Growth medium	N	P	K	Ca	Mg	Mn	Fe
				Percent			
Field (unfertilized)	2.96	0.23	0.85	0.64	0.19	0.01	0.01
Pot culture (unfertilized)	1.95	.13	1.25	1.07	.23	.95	.05
Deficiency levels[1]	2.4	.16	.4	.08	.11	not determined	

[1] *Guideline values from Table 4.*

out the study. A difference in phosphorus status between seedlings grown in pots and seedlings grown in the field (Table 5) could have resulted from differences in the microbial status of the two soil environments. The manganese toxicity in pot culture seedlings, also not evident in field grown seedlings, presumably developed with reducing conditions in the soil early in the study. Readily available manganese ions (bivalent) were apparently released from insoluble manganic oxides.

Growth of red alder seedlings was significantly depressed with the addition of 600 pounds per acre of nitrogen as ammonium nitrate, and a phosphorus deficiency was aggravated, as indicated by the low foliar percentages in Table 6. Several reasons may be offered to explain this depressing effect. Uptake of phosphate anions may have been depressed by competition with the rapidly absorbable nitrate anions (Arnon, 1953); phosphorus availability may have been reduced by higher soil acidity associated with the nitrogen amendments (Table 7); with increased supplies of available nitrogen the critical level of phosphorus may have been increased (Boszormenyi, 1958). Undefined trace element deficiencies and/or toxicities, other than manganese, may also have occurred in the highly acid soils of treatments receiving nitrogen amendments.

Another effect of the ammonium nitrate addition was to eliminate nodule development. None of 72 seedlings receiving nitrogen amendments developed nodules. In contrast, 21 out of 24 seedlings which did not receive nitrogen amendments developed nodules in the same soil. Since the nitrogen status of seedlings receiving nitrogen amendments is high it does not appear that lack of nodulation should have reduced growth of these seedlings. No evidence has been reported which indicates that nodules play any role in nutrition other than to supply nitrogen.

Those pots receiving phosphorus showed a response which was no doubt in part attributable to P, but since in the end total P uptake was not much

TABLE 6. Foliar composition of red alder seedlings from the fertilizer treatments

Treatment	Yield of seedlings	N	P	K	Ca	Mg	Mn	Fe
	Grams	----------------- *Percent* -----------------						
"Control"	32.02	1.95	0.13	1.25	1.07	0.23	0.95	0.05
$P_{3.5}$	50.10	2.10	.14	1.23	.90	.21	.46	.03
N_6	7.56	3.92	.09	.90	.74	.17	.90	.02
$N_6 P_{3.5}$	15.44	3.36	.11	- -	- -	- -	- -	.02
$N_6 P_{3.5} S$	14.09	3.63	.11	- -	- -	- -	- -	.02
$N_6 P_{3.5} K_2 S$	12.13	3.51	.09	1.12	- -	- -	.81	.02
$N_6 P_{3.5} K_2 SCa$	27.10	3.02	.10	1.01	1.08	.19	.48	.02
$N_6 P_{3.5} K_2 SCaMg$	13.92	3.47	.09	- -	- -	.23	.49	.01

higher, secondary effects of this fertilization were probably of more importance. Total phosphorus uptake by the foliage of amended seedlings was 0.17 grams versus 0.14 grams in unfertilized seedlings. It does not seem likely that these differences alone could account for the significant growth response to the phosphorus amendment. Favorable secondary effects may have been more important. These were: larger nodules and improved nitrogen fixation and uptake; reduced manganese content; and slightly less soil acidity. The percentage of foliar nitrogen was higher in the phosphorus amended soil (2.10 versus 1.95 percent) as was total nitrogen uptake by the foliage (0.254 versus 0.189 grams). Nodules in the treatment receiving 350 pounds per acre of phosphorus were twice as large as in the unfertilized treatment (0.08 versus 0.04 grams per nodulated seedling). Larson (1964) concluded that most investigators working on acid soil have found that phosphate application decreases manganese uptake by plants.

TABLE 7. Relations between soil pH and yield in fertilizer treatments

Fertilizer	Treatment yield	Soil pH
	Grams	
$P_{3.5}$	50.10	5.1
"Control"	32.02	5.0
$N_6 P_{3.5} K_2 SCa$	27.10	4.8
$N_6 P_{3.5}$	15.44	4.3
$N_6 P_{3.5} S$	14.09	4.5
$N_6 P_{3.5} K_2 SCaMg$	13.92	4.7
$N_6 P_{3.5} K_2 S$	12.13	4.3
N_6	7.56	4.2

In treatments receiving both phosphorus and nitrogen, growth and uptake was dominated by the depressing effect of the nitrogen fertilizer. Except when calcium was added, application of both nitrogen and phosphorus resulted in significantly smaller seedlings than in the unfertilized treatment.

In the presence of a nitrogen amendment the addition of calcium significantly increased growth. Since foliar percentages did not indicate that calcium was deficient in any pot culture treatment, the response must have been due to secondary effects of the calcium addition. These were reduced soil acidity and reduced manganese level. A comparatively low nitrogen/phosphorus ratio in the calcium treatment may also have been important by reducing the severity of the phosphorus deficiency. The reason for this low ratio was not apparent, however.

Potassium and sulfur fertilizers produced no alteration of the growth responses when applied in combination with the nitrogen fertilizer. The magnesium addition resulted in very poor growth. Five seedlings in this treatment were dying when the seedlings were harvested. Not more than one seedling in any other treatment was dying at this time.

Summary

Guidelines were developed in the sand culture experiment for assessing deficiencies of nitrogen, phosphorus, potassium, calcium, and magnesium in red alder seedlings. These guidelines proved useful in interpreting results of a pot culture study. Differences in nutrient status were indicated between unfertilized pot culture seedlings and unfertilized seedlings grown in the field on the Lynden loam soil. Knowledge of these differences was of value in avoiding incorrect conclusions concerning the potential applicability of this pot culture trial to field growth of red alder.

In both sand and soil media, nodule development was retarded by the addition of combined nitrogen. With the addition of 600 pounds per acre of nitrogen as ammonium nitrate, nodules did not develop. Although nodulation frequency was high in the pot culture seedlings which did not receive nitrogen fertilizer, these nodules were not effective in supplying nitrogen to the seedlings. This was in contrast to the very effective nodules in the low nitrogen treatments in the sand medium. The ineffectiveness of the nodules in the pot culture study may have been due to insufficient oxygen supplies in the sieved and potted soil. Ferguson and Bond (1953) concluded that *Alnus glutinosa* nodules had higher oxygen requirements than the roots. MacConnell (1959) concluded that oxygen supply is of special importance in the development and function of the alder nodule.

The guidelines for assessing deficiencies proved useful in evaluating fertilizer responses in the pot culture study. Growth of red alder seedlings was significantly depressed with addition to the soil of 600 pounds per acre of nitrogen as ammonium nitrate. A phosphorus deficiency was aggravated by the nitrogen fertilizer. Other adverse effects were produced with the addition of the nitrogen fertilizer since soil acidity was appreciably increased and Mn uptake stimulated. Favorable responses of red alder seedlings to phosphorus

and calcium fertilizers in the pot culture study may have resulted chiefly with the relief of artificial deficiencies and toxicity induced by the pot environment.

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Photosynthesis of red alder, Douglas-fir, Sitka spruce, and western hemlock seedlings

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Abstract

More rapid growth by red alder seedlings than by associated coastal conifers creates interest in their comparative photosynthetic behavior. Seedlings of the four species, previously grown under light and heavy shade, were brought to the laboratory at intervals during their second growing season for measurement of photosynthetic rate by infrared CO_2 analysis at five light intensities.

Photosynthetic rates expressed on a leaf-area basis did not differ greatly between species up to saturating light intensities for the conifers. The conifers, especially western hemlock, reached maximum rates at lower light intensities than did alder. Growing the four species under heavy shade tended to decrease species differences in photosynthetic rates.

The distribution of plant weight between photosynthetic and nonphotosynthetic tissue was generally similar for all species. Alder produced more leaf area per unit weight of leaf, however. In the dark, respiration rate per gram of top was highest for alder.

Greater capacity to utilize high light intensities for photosynthesis combined with more area per unit weight of leaf and greater total leaf area per seedling may contribute substantially to alder's faster growth in high light situations.

Detailed results of this study will be reported elsewhere.

Enzyme systems of red alder and Douglas-fir in relation to infection by *Poria weirii*[1]

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Abstract

Poria weirii *hyphae secreted compounds, presumably phenoloxidases, that resulted in oxidation of catechol, DL-dopa, and hydroquinone but not P-cresol. Phenoloxidases with similar activity were found in red alder leaves but were lacking in Douglas-fir leaves. Leaves of both alder and Douglas-fir showed peroxidase activity, but at much higher levels in alder than in fir. Alder leaves were able to reduce nitrate nitrogen, presumably through presence of nitrate reductase, whereas leaves of Douglas-fir lacked apparent nitrate-reducing ability.*

These preliminary studies will be followed by studies on wood and roots of alder and Douglas-fir. If, as is likely, the phenols and phenoloxidase system in red alder leaves are also present in roots, a reason for alder's resistance to Poria weirii *can be hypothesized. On penetration by the fungus, the* o-*dihydric phenols in alder tissue would be oxidized into fungitoxic compounds through the catalytic action of the phenoloxidases. These compounds, deposited about the periphery of the initial infection, would inhibit further spread of the fungus. Peroxidase activity, too, might contribute to resistance. Nitrate reductase activity assumes possible importance in that* Poria weirii *cannot reduce nitrate, whereas many of its antagonists can. Thus, the high nitrate levels in stands containing alder are not directly usable by* P. weirii *but permit buildup of high populations of antagonists.*

Introduction

Red alder *(Alnus rubra* Bong.) is resistant to infection by *Poria weirii* Murr., one of the major root pathogens of conifers in western North America (Wallis and Reynolds, 1962 and 1965). In this paper, we report studies on (1) phenoloxidases, peroxidase, and nitrate reductase activities in red alder as compared to Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco), and (2) some phenols that are oxidized by phenoloxidases produced by *P. weirii.* The possible role of these enzyme systems in resistance of alder to *P. weirii* infection is hypothesized.

Certain phenoloxidases in wood-rotting fungi are related to lignin-decomposing ability (Etheridge, 1957; Käärik, 1965; Lindeberg, 1948; Scháněl, 1967). *P. weirii* is a lignin decomposer, producing a yellow ring rot in conifer wood; when grown on gallic or tannic acid media, it produces a brownish diffusion zone (Nobles, 1948), indicating presence of phenoloxidases. On the other hand, activity of other phenoloxidases in higher plants has been related to browning of injured tissues (Burges, 1963; Sisler and Evans, 1958) and to defense against parasitic infection (Hare, 1966; Rubin and Artsikhovskaya, 1963).

The literature on phenolic content of Douglas-fir and red alder tissue is scant, but some leads on compounds of possible importance in resistance to *Poria weirii* appear in the compilations of Hegnauer (1962, 1964). Leaves of both species contain quercetin kaempferol, and myricetin. If present also in roots of both, these compounds would not account for differences in resistance between the two. The compounds taxifolin (which oxidizes to quercetin), catechin, and epicatechin, occurring in bark of Douglas- fir and other *Poria*-susceptible trees such as *Tsuga* spp., similarly do not appear to inhibit penetration by *P. weirii*. On the other hand, leaves of red alder contain compounds which have not been reported from Douglas-fir: chlorogenic, caffeic, gallic, and protocatechnic acids. Moreover, red alder wood and bark contains a phenolic xyloside that is responsible for the reddening of freshly exposed wood, and its bark contains taraxerol and teraxeron. Chlorogenic, caffeic, gallic, and protocatechnic acids or products of their oxidation as catalyzed by phenoloxidases are fungitoxic and are implicated in disease resistance of a number of plants, as are catechol and several other phenols and quinones (cf. Hare, 1966).

High peroxidase activity is related to field resistance of potatoes to blight caused by *Phytophthora infestans* (Mont.) deBary (Fehrmann and Dimond, 1967; Umaerus, 1963). Its role in resistance of tree roots to pathogenic infection is unexplored.

Activity of nitrate reductase, the enzyme necessary for assimilation of nitrate ions, has not been heretofore determined for either red alder or Douglas-fir. Studies of *P. weirii*, however, have shown that it cannot use nitrate and lacks nitrate reductase (Li et al., 1967).

The studies reported in this paper are preliminary in respect to the role of enzymes in resistance of trees to infection by *Poria weirii*, because enzyme activities were determined for leaf rather than root tissue of alder and Douglas-fir (leaves were easier to work with in developing techniques and in gaining initial data). Further studies will follow on root tissue, which likely, but not necessarily, contains the same or similar enzyme systems.

Materials and Methods

DETECTION OF SPECIFIC EXTRACELLULAR PHENOLOXIDASES PRODUCED BY *PORIA WEIRII*

A culture of *P. weirii* was grown in 250 ml of liquid synthetic medium (Table 1 of Trione, 1964, but substituting 10 gm glucose for sucrose). After

3 weeks of growth, 10 ml aliquots of the medium were pipetted into each of 18 Erlenmeyer flasks. The medium in 8 of the flasks was boiled to inactivate enzymes for controls. Meanwhile, solutions of the phenols *P*-cresol, DL-dopa, catechol, and hydroquinone were prepared at concentrations of 2.75 mg/ml double-distilled water and sterilized by glass filtration. Two ml of each phenol solution were then added to each of two flasks containing boiled and unboiled aliquots of medium on which *P. weirii* had been grown, while similar amounts of distilled water alone were added to two flasks of unboiled medium as additional controls. Brown to black discoloration of the mixtures indicated activity of enzymes on the specific phenols.

EXTRACTION OF PHENOLOXIDASES
FROM RED ALDER AND DOUGLAS-FIR

The extraction procedure was essentially the same as that of Badran and Jones (1965). Four gm of leaves were collected from 2-year-old, greenhouse-grown trees and washed in cold, redistilled water. The leaves were cut into small fragments while immersed in 100 ml 0.1M-potassium phosphate buffer at pH 6.5, containing 1 percent polyethylene glycol (PEG), molecular weight 4,000 (Carbowax 4000, Union Carbide Chemicals Company). The fragments were vacuum infiltrated for 30 minutes, then removed and added to another 40 ml PEG-buffer solution. This mixture was homogenized in an Omni-Mixer at maximum speed for 3 minutes, after which the homogenate was poured into 80 ml cold acetone (-20°C), and centrifuged at 1,200 g for 10 minutes. The precipitate was immersed for 30 minutes in 20 ml of 0.1M-potassium phosphate buffer, pH 6.5, to solubilize the enzymes, and centrifuged at 3,000 g for 10 minutes. The supernatant was decanted and recentrifuged at 18,000 g for 10 minutes. The final supernatant was then tested for poly-phenoloxidase activity.

The assay mixture contained 0.1 ml enzyme extract and 2.9 ml of 10^{-3} M substrate — catechol, chlorogenic acid or DL-dopa. The reaction was followed by measuring light absorption at 15-second intervals in a Beckman DB spectrophotometer at 400 mμ for chlorogenic acid and catechol and at 495 mμ for DL-dopa. This 0.1 ml enzyme extract represented the enzyme activity per 18 mg fresh leaf tissue.

EXTRACTION OF PEROXIDASE FROM
RED ALDER AND DOUGLAS-FIR

Six g of leaves of each species were collected from 2-year-old greenhouse-grown trees. The leaves were washed in cold, redistilled water and stored in a cold room at 0°C for 18 hours. They were then homogenized with 50 ml buffer at pH 7.0 (McIlvaine, 1921) containing 10^{-2} M cysteine and 6 g of dry polyclar AT (Loomis and Battaile, 1966) in an Omni-Mixer at maximum speed for 3 minutes. The homogenate was filtered through fine-mesh nylon cloth and the filtrate centrifuged at 3,000 g for 5 minutes. The clear supernatant was then tested for peroxidase activity. The assay mixture consisted of 0.5 ml enzyme extract, 0.1 ml of 0.2M pyrogallol, 1.0 ml McIlvaine's buffer, pH 7.0, 0.5 ml of 0.01M H_2O_2 and 0.9 ml redistilled water. Blanks

used in the spectrophotometric analysis were composed of the same assay mixture, but one lacked enzyme extract and the other, H_2O_2. Absorption at 430 mμ was measured at intervals of 15 seconds in a Beckman DB spectrophotometer. This 0.5 ml enzyme extract represented the enzyme activity per 60 mg fresh leaf tissue.

REDUCTION OF NITRATE TO NITRITE BY RED ALDER AND DOUGLAS-FIR

Ten grams of leaves were collected from Cascade Head Experimental Forest (maintained by the U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station), Oregon. The leaves were surface-sterilized by dipping into 2.65 percent sodium hypochlorite solution for 5 minutes and washed twice with sterile distilled water. They were then immersed for 4 days at room temperature in 600 ml Hoagland solution 1 (Hoagland and Arnon, 1938), which had been diluted to ¼ strength with sterile distilled water. This step was devised on the basis that reduction of nitrate requires the enzyme nitrate reductase (Townsend and Blatt, 1966), whose production is induced in the presence of nitrate ions (Beevers and Hageman, 1963; Raghavan and Torrey, 1964; Rijien, 1958 and 1960). Two ml of streptomycin sulfate solution (10 mg/ml) were also added to the solution to minimize bacterial growth. Nitrite released into solution was tested by adding 1.0 ml of 1 percent sulfanilamide and 1.0 ml 0.02 percent N-(1-Naphthyl) ethylenediamine hydrochloride to 2 ml test solution. After 20 minutes, the color density was read at 540 mμ on the Beckman DB spectrophotometer. Hoagland solution without leaf inoculation, and sterile distilled water with leaf inoculation were used as blanks.

Results

Extracellular compounds produced in synthetic medium by *P. weirii* resulted in the oxidation of catechol, DL-dopa, and hydroquinone. No oxidation of *P*-cresol was detected. The secreted compounds presumably included the enzymes *o*-diphenoloxidase, which catalyzes oxidation of catechol and DL-dopa, and *p*-diphenoloxidase, which catalyzes oxidation of hydroquinone.

Red alder leaves possessed phenoloxidases which catalyzed the oxidation of *o*-dihydric phenols, such as chlorogenic acid, catechol, and DL-dopa, chlorogenic acid being the most reactive substrate. The extract from Douglas-fir leaves showed no phenoloxidase activity for these three substrates (Figs. 1 and 2). Leaves of both red alder and Douglas-fir possessed peroxidase, but the former showed much higher activity than the latter (Fig. 3). Red alder leaves possessed nitrate reducing capacity and, therefore, nitrate reductase: in 4 days 1 gm of leaf tissue was able to form 0.74 μ moles of nitrite (Table 1). However, no activity was detected in Douglas-fir leaves.

Discussion and Conclusions

Poria weirii can penetrate the wood of both Douglas-fir and red alder, but in the case of alder the bark must generally be injured first. Even then,
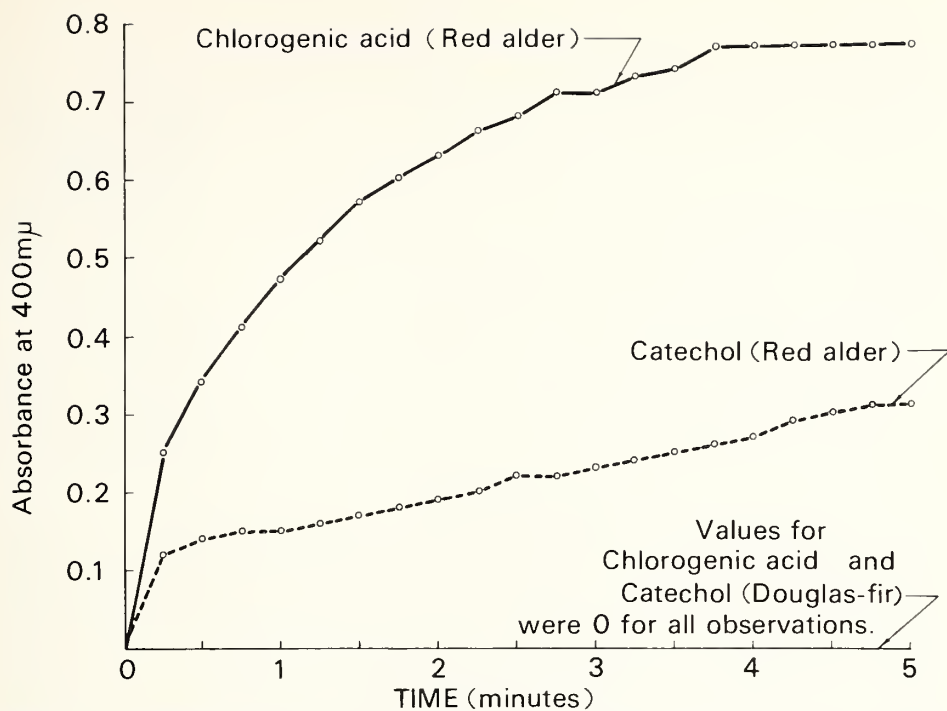
Figure 1. Phenoloxidase activity of leaf extracts obtained from red alder and Douglas-fir. Assay: substrates, chlorogenic acid and catechol $1 \times 10^{-3}M$, 2.9 cc, enzyme extract 0.1 cc.
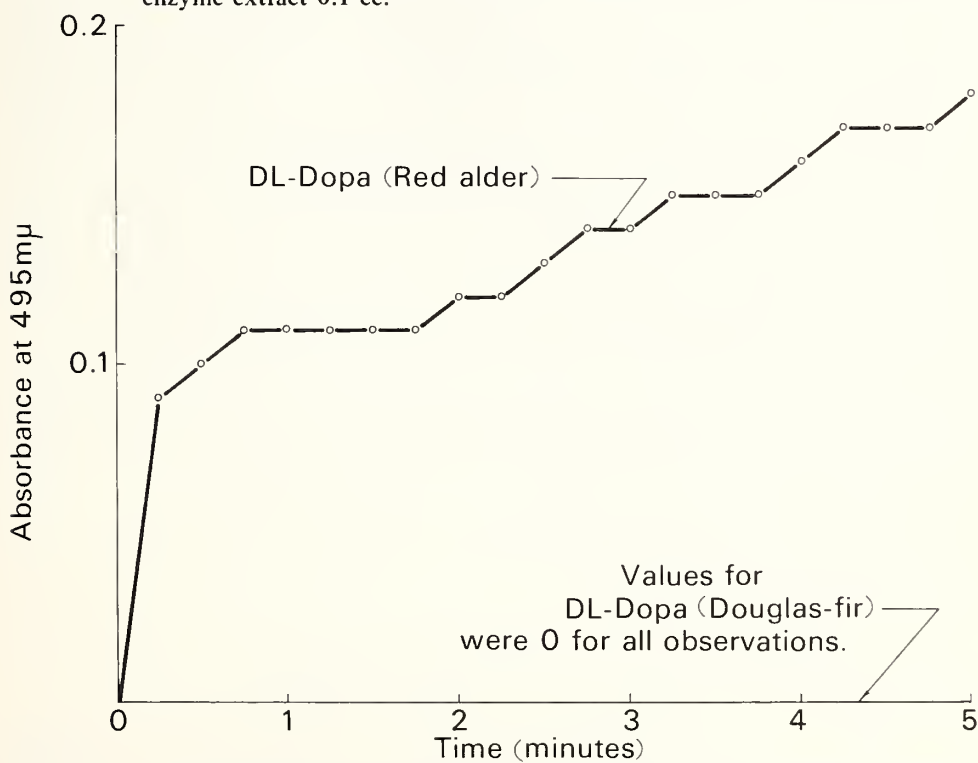

Figure 2. Phenoloxidase activity of leaf extracts from red alder and Douglas-fir. Assay: substrate, DL-dopa, $1 \times 10^{-3}M$, 2.9 cc. enzyme extract 0.1 cc.
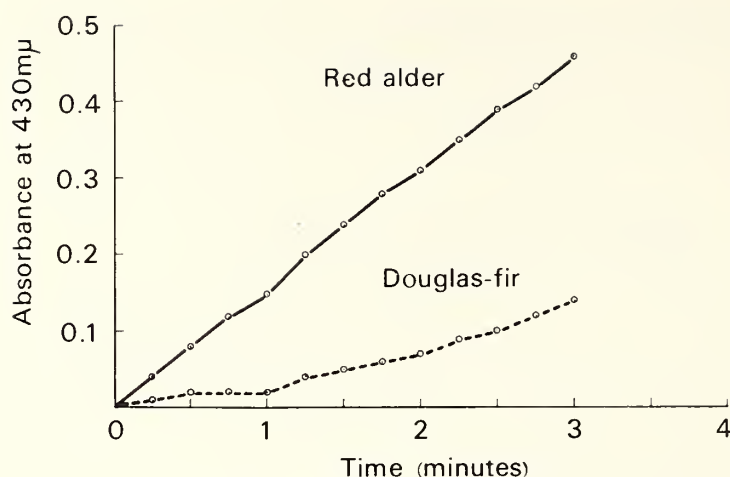
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Figure 3. Peroxidase activity of leaf extracts obtained from red alder and Douglas-fir. Assay: pyrogallol, 0.2 M, 0.1 ml, McIlvaine's buffer, pH 7.0, 1.0 ml H_2O_2, 0.01 M, 0.5 ml, enzyme extract 0.5 ml and redistilled water 0.9 ml.

growth of the fungus is restricted to a small zone around the point of entry (Wallis and Reynolds, 1964). Heat labile compounds evidently account for this resistance of alder wood to growth of the fungus: *P. weirii* will grow well in the autoclaved wood (Wallis and Reynolds, 1962), but not in previously unheated wood (G. W. Wallis, personal communication).

The heat labile compounds prominently involved in alder's resistance to *P. weirii* probably include phenoloxidases that catalyze oxidation of chlorogenic acid and other phenols in the tissue into fungitoxic end-products (Hegnauer, 1964; Rubin and Artsikhovskaya, 1964; Hare, 1966). Initial penetration by the fungus into alder wood could activate the phenoloxidases in the tissue (Byrde et al., 1960; Rubin and Artsikhovskaya, 1964). The products of phenol oxidation would then accumulate in infected cells and polymerize, forming dark, resin-like substances which impregnate the tissue and form a barrier to further spread of the mycelium (Rubin and Artsikhovskaya, 1963 and 1964). It is also possible that these or other oxidized phenols in the infected tissue inactivate or precipitate the extracellular phenoloxidases produced by *P. weirii*, thereby preventing lignin degradation by the fungus (Byrde et al., 1960; Loomis and Battaile, 1966).

TABLE 1. Reduction of nitrate to nitrite in 4 days by leaves of red alder and Douglas-fir

Species	Absorbance of test solution at 540 mμ	Nitrite formed (μ mole/g of tissue)	Mean
Douglas-fir	0	0	
	0	0	0
	0	0	
Red alder	0.385	0.770	
	.397	.794	0.784
	.390	.780	

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Red alder has high peroxidase activity, which might increase considerably in hypersensitive red alder reaction-tissue during invasion by *P. weirii* hyphae (Rubin and Artsikhovskaya, 1963 and 1964). Fehrmann and Dimond (1967) have postulated that peroxidase activity is one attribute of host tissue contributing to environmental inhospitality for a fungus.

One of the direct results of nitrogen fixation by alder nodules is a buildup of total soil nitrogen levels and, particularly, of nitrite nitrogen (Bollen and Lu, 1968). *Poria weirii* has previously been shown unable to assimilate nitrate, presumably for lack of nitrate reductase (Li et al., 1967). If our results with leaves are representative of the tree as a whole, Douglas-fir may also lack this enzyme. Red alder, in contrast, has the enzymatic ability to reduce nitrate to usable form as do many soil organisms likely to be strong antagonists of *P. weirii* (cf. Li et al. 1967). Consequently, *P. weirii* does not compete with its antagonists, such as *Streptomyces* species, for nitrate – the presence of which contributes to the buildup of antagonistic populations in presence of alder (Lu and Bollen, 1968). *P. weirii* survives relatively poorly where antagonistic and competing organisms thrive (Nelson, 1967); the circumstances of nitrogen fixation and presence or lack of nitrate reductase activity in the respective organisms can logically be expected to mitigate against *P. weirii* in stands containing alder as a major component.

To recap these interpretations, the phenols and phenoloxidases present in red alder but not detected in Douglas-fir can be hypothesized as a primary biochemical source of alder's resistance to *Poria weirii* by (1) resulting in oxidation of *o*-dihydric phenols into fungitoxins at the infection site, and (2) destroying the lignin decomposing ability of *P. weirii* by inactivating its extracellular enzymes. The relatively high peroxidase activity may further contribute to resistance against the fungus. Because *P. weirii* spreads by growth in infected root systems rather than by growth through the soil, spread from tree to tree is primarily by growth of healthy roots to an infection source (Wallis and Reynolds, 1965). The mere presence of resistant alder trees in a stand, therefore, reduces the chances for root contacts between susceptible trees. The high soil nitrate levels in stands containing alder, moreover, cannot be used by *P. weirii* but do encourage growth of organisms that antagonize or compete with it.

Additional research is planned to test these hypotheses as well as to determine whether the phenols or their fungitoxic oxidation products are present in soils of stands containing alder.

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Hypoxylon fuscum:
A review of the fungus and its relationship with *Alnus* in the Northwest

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Abstract

Hypoxylon fuscum *is a widely distributed inhabitant of* Alnus *species and other betulaceous species throughout the North Temperate Zone. The fungus causes a rapid white-type rot of wood of dead or dying* Alnus *plants. It probably is a weak parasite, possibly contributing to killing of trees. The morphology and development of the fungus and known aspects of its relationship to* Alnus tenuifolia *are discussed.*

Introduction

Hypoxylon fuscum Pers. ex Fr. is a widely distributed pyrenomycete, occurring principally on betulaceous hosts. It is exceedingly common on species of *Alnus*. Indeed, Miller (1961) probably did not greatly overstate the facts when he wrote that the "fungus is on almost every limb of *Alnus* that has recently died anywhere in the North Temperate Zone". In spite of its wide distribution and frequent occurrence, however, the fungus and its activities are not well understood. I have investigated *H. fuscum* and its relationship to *Alnus*, particularly *A. tenuifolia* Nutt., for the past 3 years. Field work has been done primarily in north central Idaho and in southeastern Washington. The objective of this paper is to review results of my studies, some of which have been published elsewhere, and the work of others.

The Fungus

DESCRIPTION

The perfect stage of the fungus has been adequately described and illustrated by Miller (1961). An abbreviated description follows:

Stromata irregular in shape, effused, applanate, or most commonly hemispherical (especially when they occur on small corticated branches), 1-5 mm (rarely 10 mm) in diameter, and 0.5-5 mm thick. Stromata typically in shades of purple gray, old stromata becoming blackish. Stromata soft to slightly brittle in old specimens. Stromal surface smooth, punctated with umbilicate perithecial openings. Perithecia small, globose to angular, com-

pletely immersed (Fig. 1). Ascospores eight per ascus, brown, 10-15 x 3-10μ elliptical with one flattened side, featuring a germ slit (Fig. 2) and an easily removable perispore.

The conidial stage covers the immature stroma prior to perithecial formation, giving it a tan color and dusty appearance. Production of conidia slows as perithecia are being produced, finally ceasing altogether as mature ascospores become evident. Conidiophores are often initiated on old stromata during wet weather, but deteriorate rapidly following the onset of drier conditions. The conidial stage has been illustrated by Chesters and Greenhalgh (1964), Rogers (1966), and others. An abbreviated description follows:

Conidiophores sympodially branched (Fig. 3), at first hyaline, becoming subhyaline to brown in older parts. Conidia formed at conidiophore tip, then pushed into lateral positions as conidiophore continues to elongate, resulting in a false head of spores. Conidiophores smooth to minutely roughened, becoming verrucose in older parts. Conidia obovate to oblong-elliptical, smooth, with truncate bases (Fig. 4), hyaline to slightly greenish in mass, (2)4-6(10) x 2-4μ. Conidial *H. fuscum* could be accommodated by the form-genera *Acrostaphylus* Arn. ex Subram. or *Nodulisporium* Preuss, depending primarily on the degree of pigmentation of the conidiophores as discussed in Rogers (1966).

Hypoxylon fuscum can be cultured readily on malt agar, potato dextrose agar with 5g/liter yeast extract and other media. The perithecial stage has never been formed on the media tested. Conidia are produced very infrequently in plate cultures. They are produced more frequently and more abundantly near the bases of test tube slant cultures (Rogers, 1966).

DEVELOPMENTAL MORPHOLOGY

A detailed account of perithecial development in *H. fuscum* will be published elsewhere. The essentials are as follows. A deep-staining ascogonial coil becomes evident immediately beneath the ectostroma, i.e. the outer stromal layer with its attending conidiophores. The coil becomes enveloped by hyphae of narrower diameter (Fig. 5), this envelope eventually becoming the ascocarp wall. The coil continues to develop, producing branches and loops. Coil hyphae are sparsely septate, each cell containing one or more nuclei. The ascogonial coil hyphae then undergo a dramatic change. They become segmented, falling apart at the septa into what appear to be individual cells (Fig. 6).

Concomitant with ascogonial segmentation, the envelope increases in size and becomes pyriform owing to hyphal growth oriented toward the ectostroma. Owing to the change in size and shape of the envelope, the relative position of ascogonial cells changes, i.e. from their former central location to the lower third of the ascocarp initial. Hyphae originating from the inner wall of the envelope grow inward, keeping pace with the expanding envelope. These hyphae probably function in ascocarp expansion and are thus called space-making hyphae.

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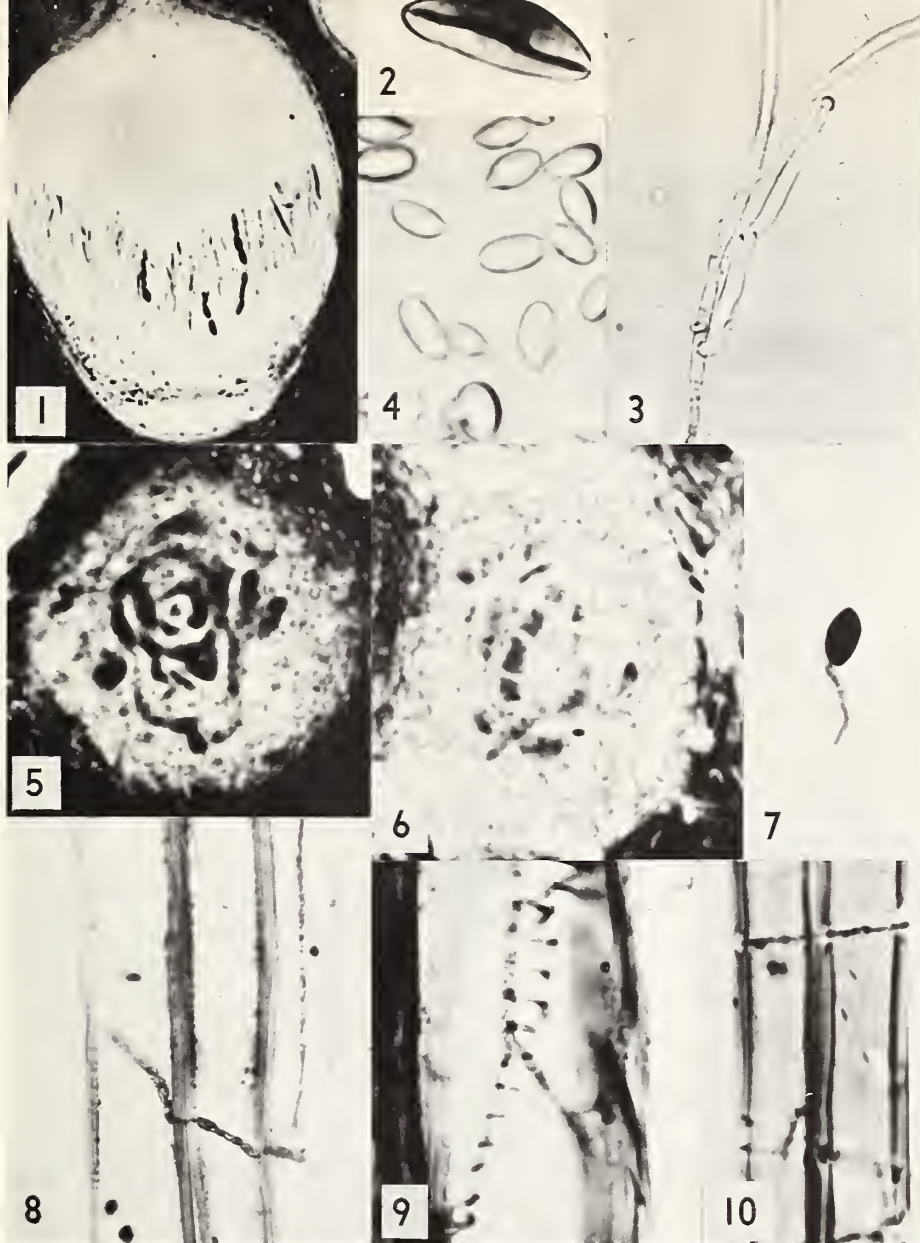
Figures 1-10. *Hypoxylon fuscum*: **1,** Young maturing perithecium. Note scattered mature asci with dark-colored ascospores. (Rotary miscotome section, iron alum hematoxylin stain; ca. X 133.) **2,** Maturing ascospore that has not yet attained its full brown color. Crushed slightly to show germ slit (dark line running the length of the spore). (HC1-Giemsa stain; ca. X 2,800.) **3,** Conidiophore. Note very minute warts. (Unstained water mount; ca. X 1,300.) **4,** Conidia. (Unstained water mount; ca. X 1,400.) **5,** Ascogonial coil surrounded by lighter enveloping hyphae. (Rotary microtome section, iron alum hematoxylin stain; ca. X 874.) **6,** Segmented ascogonial coil hypha. (Rotary microtome section, iron alum hematoxylin stain; ca. X 500.) **7,** Germinated ascospore. (HC1-Giemsa stain; ca. X 937.) **8,** Hypha traversing walls of three fibers. Note constrictions of hypha in walls. (Maceration, safranin stain; ca. X 750.) **9,** Branching hypha passing through scalariform perforation plate of vessel (side view). (Sliding microtome section, picro-aniline blue stain; ca. X 750.) **10,** Hypha passing through fiber walls. Note that diameter of bore hole has become larger than hypha. Note empty bore hole just above numeral. (Maceration, safranin stain; ca. X 750.)

The derivatives of the ascogonium, now in the base of the ascocarp, are of two kinds — large, thin-walled cells of uncertain function, called secondary ascogonial cells, and much smaller cells, the ascogenous cells. The cytology of these cell types has been discussed elsewhere (Rogers, 1965).

The envelope continues to expand, and the layer of ascogenous cells comes to cover the base of the young ascocarp. The manner by which ascogenous cells proliferate is not clear. A short ostiole is formed at the apex of the ascocarp by the opposing growth of deep-staining hyphae, the periphyses, which eventually rupture the ectostroma.

Short hyphae are produced from ascogenous cells, these ascogenous hyphae terminating in typical croziers. Asci arise from croziers in the manner described for many other ascomycetes (see Alexopoulos, 1962; Rogers, 1965). The young asci grow into the more or less solid mass of space-making hyphae, lysing some of it. The space-making hyphae that escape lysis remain intermingled with the asci and are called paraphyses.

CYTOLOGY

Cytological aspects of asci of *H. fuscum* have been investigated by Rogers (1965). Karyogamy occurs in the penultimate cell of a crozier. Homologous chromosomes synapse in a highly contracted condition. As the ascus develops from the penultimate cell and enlarges, the chromosomes elongate. They continue to elongate until they resemble the pachytene chromosomes of most other organisms, i.e. no zygotene or leptotene configurations are encountered. Normal diplotene contraction is followed by other phases of division I of meiosis. Division II of meiosis and a mitosis ensue, resulting in an eight-nucleate ascus. The haploid chromosome number of *H. fuscum* is four, based on counts at meiotic and mitotic metaphases.

An ascospore is formed around each of the eight nuclei in an ascus. Ascospores of *H. fuscum*, unlike those of some other *Hypoxylon* species (Rogers, 1965), are normally uninucleate from formation to maturity. Maturing ascospores are surrounded by a hyaline outer wall, the perispore, which becomes evident during germination or in crushed spores.

SEXUALITY

It is not known whether or not fertile ascocarps of *H. fuscum* can be formed on a thallus resulting from a single germinated ascospore, i.e. whether the fungus is hetero- or homothallic. I have hypothesized that the conidia of *H. fuscum* are, in fact, spermatia. However, developmental studies have not revealed a trichogynous extension of the ascogonium, usually considered as a necessary receptive structure for functional spermatia. Thus, if conidia do function as spermatia, their *modus operandi* is obscure.

Other evidence, derived from culturing the fungus on branch segments in a growth chamber (see later), suggests that the fungus is indeed homothallic. However, the experiments need to be repeated before the question of sexuality can be answered with certainty.

Life History and Pathogenesis on *Alnus*

GENERAL RELATIONSHIP TO *ALNUS TENUIFOLIA*

Hypoxylon fuscum causes a rapid, white-type rot on recently killed *Alnus*, attacking both sapwood and heartwood. It is among the first fungi to invade dead branches and boles. It undoubtedly is the most common wood-rotting ascomycete, probably the most common wood-rotting fungus of any type on *A. tenuifolia* in the southeastern Washington — north central Idaho area.

There is a growing suspicion that the fungus invades the tree, probably smaller branches, prior to the tree's death. This suspicion grows out of the observation that stromata of the fungus are sometimes encountered on very recently killed branches. It is known that the fungus requires 6-8 weeks to produce conidial stromata (12-20 weeks for mature perithecial stromata) on artificially inoculated *A. tenuifolia* branch segments in a growth chamber (see later), i.e. the fungus must produce a certain amount of vegetative growth prior to fruiting. It is considered possible that the fungus invades unthrifty branches and contributes to their killing, fruiting shortly after their death.

Evidence for *H. fuscum* invading living *Alnus* in the field is lacking. Several hundred inoculations of living and dead *A. tenuifolia*, by a variety of techniques and under various conditions, have not resulted in success. It is suspected that the conditions for natural infection of living or dead *Alnus* are very specific; these conditions have not yet been met in my studies. This is not surprising in that natural infection phenomena by *H. pruinatum* (Klotzsch) Cooke [=*H. mammatum* (Wahlenb.) J. H. Miller] and *H. punctulatum* (Berk. and Rav.) Cooke, much-investigated invaders of *Populus* and *Quercus*, respectively, have not been solved (although reliable artificial inoculation procedures have been worked out after considerable effort) (Berbee and Rogers, 1964; Davis, 1966). Efforts to find a reliable inoculation procedure for *H. fuscum* continue. A breakthrough would eliminate a major "bottleneck" to many needed field studies.

POTENTIAL SOURCES OF INOCULUM

Ascospores are undoubtedly the most important, if not the only, natural inoculum. Ascospores germinate within 24 hr after their ejection from stromata onto plates of common media (Rogers, 1965). Incubation has been accomplished at room temperature, either in intermittent light or darkness. Germination proceeds as follows. The ascospore swells, breaking the perispore near the center of the spore. One or more germ tubes emerge from the germ slit (Fig. 7), often pushing the perispore some distance from the spore (Rogers, 1965).

Stromata bearing mature ascospores of *H. fuscum* are present at all seasons in *Alnus* stands. The seasonal periodicity of their release is not known, but Ingold (1965) speculates that stromata under natural conditions of alternate wetting and drying, warming and cooling, probably remain active for only a single season of not more than 6 months. I routinely keep stromata

until needed in a laboratory cold room under fairly dry conditions. Stromata collected 3 years ago continue to eject ascospores, following immersion for 2-4 hr in water and subsequent drying beneath a petri plate. Ingold (1965) has stored stromata of *H. fuscum* over anhydrous calcium chloride in a refrigerator. After 18 months, perithecia discharged spores within 1-2 days after rehydration.

Ingold (1965) and Walkey and Harvey (1966) have shown conclusively that light, even at very low intensities, has an almost immediate inhibitory effect on ascospore discharge. These investigators call *H. fuscum* a "nocturnal" species with regard to ascospore ejection.

It seems highly probable that the combination of drought-resistant (moisture conserving?) stromata, nocturnally ejected ascospores, and readily germinating ascospores is a key to unraveling natural infection. Ascospores are ejected at night and probably carried by wind to a suitable substrate. Night dews probably assure adequate moisture for ascospore germination during many days of summer. Germ tubes probably become established in appropriate infection courts within a day following germination. The riddle of a satisfactory infection court remains to be solved.

Conidia probably do not constitute important inocula. They germinate poorly under the variety of conditions tested. I speculate that they are vestigial spermatia, presently serving neither a reproductive nor a major propagative function. This theory remains to be tested adequately.

PATHOLOGICAL HISTOLOGY

The information to follow is a summary of results to be published in greater detail elsewhere. Studies on the relationship of *H. fuscum* to *Alnus tenuifolia* were performed on wood collected from naturally infected trees and from artificially inoculated branch segments incubated in a growth chamber. Wood was prepared for microscopic examination by chemical maceration and by sectioning it unembedded and embedded in paraffin and celloidin. A variety of stains – but principally picroaniline blue, safranin, and Pianeze III b – were used.

All wood cell types are attacked by *H. fuscum*. Hyphae invade cells both directly or via pits, usually becoming notably constricted on entering the wall (Fig. 8). Hyphae are of two kinds – fine hyaline hyphae developing from ascospore germ tubes and coarse brown hyphae developing from the fine type (probably a consequence of hyphal aging). Additional fine hyphae then originate as branches from coarse hyphae.

Hyphae advance most rapidly parallel to the long axes of the tissue systems involved. They advance primarily by way of the scalariform perforation plates between contiguous vessel segments (Fig. 9). Cell walls apparently are degraded via gradual thinning and erosion (Fig. 10), a phenomenon noted in some other xylariaceous fungi as in Merrill et al. (1964).

Conspicuous zone lines are formed in wood held under high moisture conditions. The dark color is due to the dark inflated hyphae in the zone and to the brown color imparted to the wood cell walls and contents (see Camp-

bell, 1933; Panisset, 1929, for studies of zone lines of other xylariaceous fungi).

Bark of *A. tenuifolia* does not feature abundant hyphae until the wood has been heavily invaded. Conspicuous masses of hyphae are first encountered in the secondary phloem and, particularly, in the cortex. In time cortical and phloem parenchyma and sieve tubes are decayed and reduced to highly staining amorphous masses. Sclereids and the periderm (at least the phellem) seem more or less immune to degradation.

Stromal formation occurs as follows. Rope-like aggregations of fine-diameter hyphae pass through breaks in the cortical sclereid band and emerge by rupturing the periderm. These hyphae then spread out on the periderm surface, forming ultimately a cushion-shaped stroma connected to the internal hyphal system by the comparatively narrow "rope". Stromata forming on decorticated wood are flattened and effuse, lacking the cushion shape. Young stromata are covered with a conidial layer from their inception.

Growth Chamber Studies

Although field inoculation studies involving *H. fuscum* and *A. tenuifolia* have yielded only negative data, it has been possible to obtain all stages of the fungus on artificially inoculated material incubated in a growth chamber. Living branches (½-1½ inches in diameter are cut into 10-inch lengths, surface-sterilized with 95 percent ethanol followed by flaming, and sealed against unnecessary water loss by dipping the cut ends in paraffin. Branch segments thus prepared are inoculated by either (1) removing a 1-cm disc of bark and inserting a 1-cm agar disc bearing mycelium against the cambium or (2) placing a drop of ascospore suspension into a deep wound made with an increment hammer. Inoculations are covered with a square of double-thickness waxed paper sealed at the edges with masking tape. Inoculated segments are put into polyethylene bags into which 2-3 ml of distilled water has been added; the top is closed with a rubber band. Incubation is accomplished in a growth chamber at 18-21°C in intermittent light.

Branch segments become heavily invaded 4-6 weeks following inoculation. Conidial stromata are produced in 6-10 weeks; mature perithecia are abundant after 12-20 weeks.

Preliminary host-range work has been done. Cultures derived from ascospores collected from *A. sinuata* (Regel) Rydb. have been successfully inoculated to *A. tenuifolia*. The *A. sinuata* from which collections were made was geographically isolated from *A. tenuifolia*. It is tentatively concluded that a given isolate of *H. fuscum* can invade wood of at least two *Alnus* species and probably others. Future work will be done with other *Alnus* species and with other betulaceous and non-betulaceous hosts.

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The effect of cobalt and certain other trace metals on the growth and vitamin B_{12} content of *Alnus rubra*[1]

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Abstract

An investigation has been made of the effects of increasing concentrations of Ni, Fe, and Mn on the growth and on the chlorophyll, N, vitamin B_{12}, and Co contents of Alnus rubra *in the presence and absence of 50 ppm Co in the nutrient medium. The effects of the Mn, Fe, and Ni on growth, both in the presence and absence of Co, were not statistically significant. At the first harvest (144 days after being placed in culture), the effects of the Co treatment on dry and fresh weights of plant tops, on the chlorophyll content of leaves, and the N content of tops were highly significant. However, at the final harvest (after 213 days in culture), the plants apparently had obtained sufficient Co from contaminating sources to satisfy most of their requirements; thus, no appreciable responses to Co addition were apparent.*

The effects of the heavy metal additions on the vitamin B_{12} content of nodules were striking and statistically significant. From the B_{12} analyses, it appeared that increasing concentrations of Ni, Fe, or Mn resulted in marked decreases in the biosynthesis of vitamin B_{12} in nodules. This was most pronounced where 0.05 ppm of Co was added to the nutrient solution and where the lowest increments of Ni, Fe, or Mn were added. The highest concentrations of these trace elements (Ni, Fe, and Mn) were associated with an increase in the B_{12} content of nodules. This increase was attributed to Co impurities in Ni, Fe, and Mn salts. In general, the effects of increasing concentrations of Ni, Fe, and Mn in nutrient solutions on Co uptake by alder tissues were similar in trends to those exhibited by effects of added metals on the B_{12} content. It is concluded that excessive Ni, Fe, and Mn may competitively interfere with the incorporation of Co into B_{12} compounds.

Introduction

Cobalt has proven to be essential for the symbiotic growth of legumes (Ahmed and Evans, 1959, 1961; Reisenauer, 1960; Delwiche et al., 1961)

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and for *Rhizobium* species grown in pure culture (Lowe and Evans, 1962). No definite requirement for cobalt has been established, however, for leguminous or non-leguminous plants grown in culture media supplied with adequate N in the nitrate or ammonium form. The concentration of B_{12} compounds in the nodules of soybeans has been positively correlated with the Co supply in nutrient media (Ahmed and Evans, 1961), and the B_{12} coenzyme (5,6-dimethylbenzimidozolylcobamide coenzyme) has been isolated and identified in cultures of *Rhizobium meliloti* and in the bacteroids from nodules of soybean plants. The structure of the compound isolated from *Rhizobium meliloti* is shown in Figure 1. By use of an enzyme assay, B_{12}
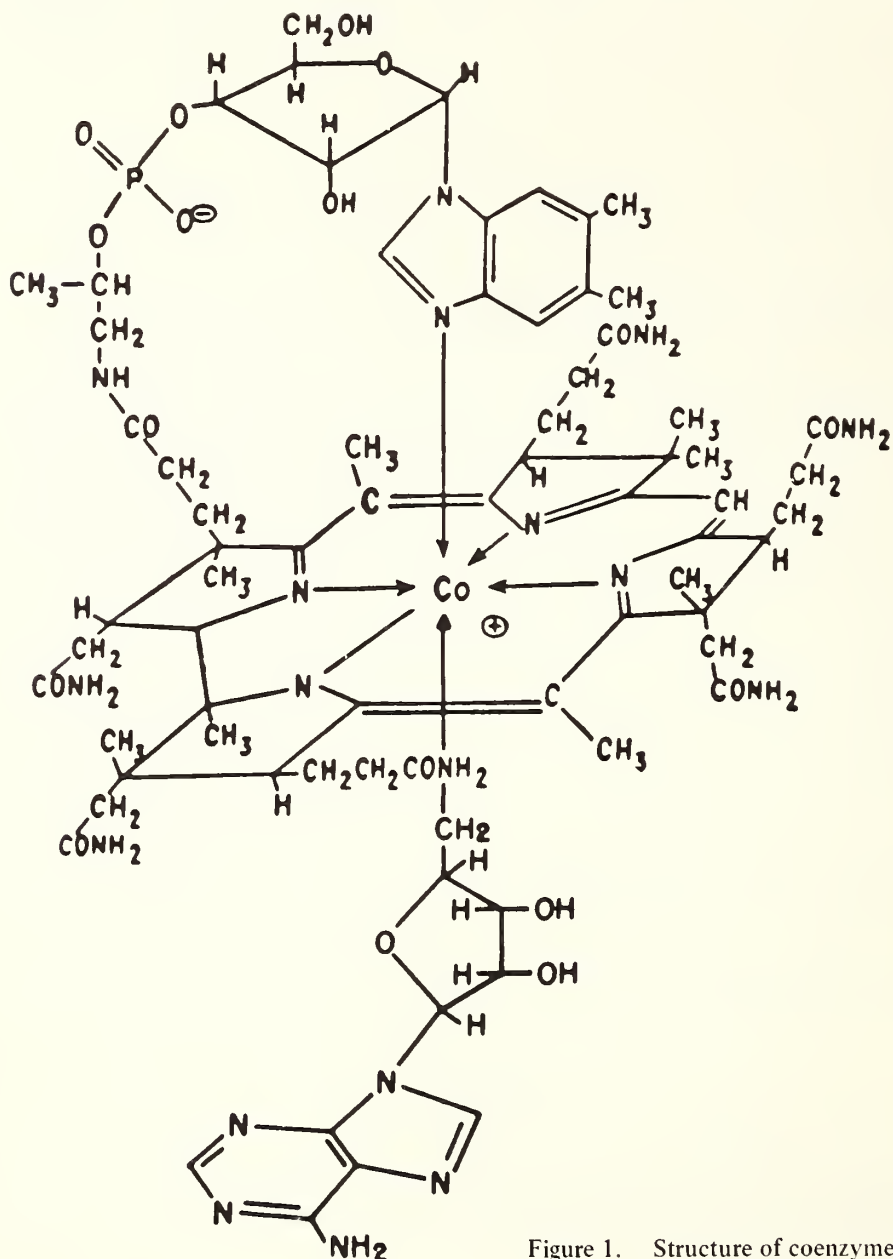

Figure 1. Structure of coenzyme B_{12}.

coenzyme(s) was identified in nodules of *Alnus rubra, Ceanothus velutinus* and a variety of leguminous species (Kliewer and Evans, 1962, 1963). From the evidence available it seems highly probable that the essential role of Co in the nutrition of nitrogen-fixing organisms is related at least in part to the role of the vitamin B_{12} coenzyme(s) that are known to contain Co as an essential component of their structure.

The research on the requirement and biochemical role of Co in leguminous species and *Rhizobium* has led to an interest in Co requirements for non-leguminous symbionts that fix atmospheric N. Bond and Hewitt (1962) showed a very definite beneficial effect of Co on the growth of *Alnus glutinosa* and *Casuarina cunninghamiana*. In 1965, Bond, Adams and Kennedy reported the detection of considerable quantities of vitamin B_{12} analogues in nodules of *Casuarina cunninghamiana, Hippophae rhamnoides, Alnus glutinosa* and *Myrica gale*. Hewitt and Bond (1966) suggested that the formation of these B_{12} compounds occurred in the endophytes of the root nodules. From these results and those summarized in a review by Evans and Kliewer (1964), it appears that Co is essential for growth of all organisms that fix atmospheric N.

Since the only known role of Co in the metabolism of organisms is associated with the essentiality of the element as a constituent of vitamin B_{12} compounds, it was desired in this investigation to determine whether the concentration of certain trace elements with chemical properties similar to those of Co might interfere with the biosynthesis of vitamin B_{12}-containing compounds in nodules of *Alnus rubra*. It seemed logical to postulate that metals such as Mn, Fe, or Ni at high concentrations might compete with Co in the incorporation of this element into the corrin moiety of B_{12} compounds. This would lead to a decreased concentration of vitamin B_{12} compounds and thus an antagonism between excessive concentrations of certain trace elements and Co.

Materials and Methods

Seed of *Alnus rubra* Bong., kindly supplied by Dr. Michael Newton of Oregon State University, were germinated in flats of acid-washed quartz sand. The seedlings were supplied with a ¼-strength nutrient solution. The concentrations of essential macroelements in moles per liter of the full strength solution were as follows: K_2SO_4, 0.0016; $MgSO_4$. $7H_2O$, 0.002; KH_2PO_4, 0.00017; K_2HPO_4, 0.00083; $CaSO_4$. $2H_2O$, 0.006; $CaCl_2$, 0.005; and NH_4NO_3, 0.001. The concentration of essential microelements expressed as ppm in the full strength nutrient solution were: B as H_3BO_3, 0.25; Mn as $MnSO_4$. $4H_2O$, 0.05; Zn as $ZnSO_4$. $7H_2O$, 0.05; Cu as $CuSO_4$. $5H_2O$, 0.02; Mo as Na_2MoO_4. $2H_2O$, 0.01; and Fe as FeEDDHA; ferric ethylenediamine (di-o-hydroxyphenyl) acetate 1.0. After 3 weeks, five seedlings were transferred to each of seventy-two 8-inch plastic pots filled with acid-washed quartz sand. The pots were arranged in the greenhouse as four replicates of a split-plot, randomized block. Seedlings were supplied with about 500 ml of nutrient solution identical with that used for germination of

the seedlings with the exception that the final concentration of solution was one-half strength. The nutrient solution was supplied to the plants twice daily, and the excess solution was allowed to drain into catch-pots placed directly below each of the culture pots. The temperature in the greenhouse was maintained near 80 F degrees during the day and 70 F degrees during the night. Plants were supplied with supplemental light of about 300 foot-candles at 3 feet for a 16-hour photoperiod.

For the inoculation of seedlings, about 200 g of fresh alder nodules were collected from the field, ground with a mortar and pestle in 0.025 molar potassium phosphate buffer at pH 6.8, strained through cheesecloth, and the volume brought to 2 liters with buffer. Seedlings in each of the pots were inoculated with 25 ml of the nodule suspension. After inoculation, the concentration of N, supplied as ammonium nitrate, was decreased to 2 ppm. Within one month after inoculation, nodules were evident on roots of the seedlings. At this time, the NH_4NO_3 was removed from the nutrient solutions and the treatments outlined in Table 1 were applied. The various nutrient solutions were prepared by modification of a standard full-strength minimal nutrient solution which was identical with that used for germination of the seedlings, with the exception that NH_4NO_3 was omitted and the concentrations of Ni, Mn, Fe, and Co were added as indicated by the treatments outlined in Table 1. The various trace element additions were applied as $NiCl_2 . 5H_2O$, $MnCl_2 . 4H_2O$, $CoCl_2 . 6H_2O$, and ferric ethylenediamine (di-o-hydroxyphenyl) acetate. During the first 4 weeks of the experiment, each pot was supplied with 1 liter per day of nutrient solution. The effluent was collected (in a catch-pot), was brought to volume, and recycled through the cultures each day for a period of 4 days. Cultures were subsequently flushed with distilled water, then new nutrient solution utilized. As the plants increased in size, increasing amounts of nutrient solution were supplied.

TABLE 1. Trace element variables used in experiment with *Alnus rubra*

Treatment No.	Trace element variable, 0 Co	Treatment No.	Trace element variable, 50 ppm Co
	Ppm		*Ppm*
1	0.00 Ni	1B	0.00 Ni
2	0.02 Ni	2B	0.02 Ni
3	0.20 Ni	3B	0.20 Ni
4	0.05 Mn	4B	0.05 Mn
5	0.50 Mn	5B	0.50 Mn
6	5.00 Mn	6B	5.00 Mn
7	0.10 Fe	7B	0.10 Fe
8	1.00 Fe	8B	1.00 Fe
9	10.00 Fe	9B	10.00 Fe

After a growth period of 144 days, average height of the 5 plants in each culture was recorded, a 3 g sample of fresh leaves from each culture was removed from the 7th node above the level of the culture medium, and chlorophyll contents were determined by the method of MacKinney (1941). Plants were harvested by cutting 3 inches above the level of the culture medium, fresh weights were recorded, and dry weights were determined after placing the material in a forced draft oven at 70°C for 2 days.

Axillary shoots were allowed to grow, and after the plants were 213 days old, a final harvest was made. Shoot heights, fresh and dry weights of tops and roots, and chlorophyll contents were measured.

The N content of the dry plant material was determined by the Kjeldahl procedure after the material had been ground to pass through a 40-mesh screen. Three g of fresh nodules were macerated in 22 ml of cold 0.01 molar phosphate buffer at pH 6.5. The vitamin B_{12} content of the nodule macerate was determined by use of the *Ochromonas malhamensis* method as described by Ford (1953) and Ahmed and Evans (1961). In this procedure vitamin B_{12} analogues such as cyanocobalamin and hydroxocobalamin are determined.

Results and Discussion

Effects on Growth and on Chlorophyll and Nitrogen Content

A statistical analysis of the effects of the various treatments on growth of plants, as indicated by measurements of height, fresh and dry weights, and N and chlorophyll contents revealed that the effect of the Co treatment (treatment 1 vs. 1B or 4 vs. 4B, Table 1) was statistically significant (Table 2). The effects of Ni, Mn, and Fe treatments on growth and on N and chlorophyll contents were not statistically significant. With the exception of B_{12} and the Co analyses, the detailed data that are presented are limited to comparisons of cultures with and without Co.

The effects of Co on the growth and composition of the tops of alder plants harvested after 144 days of growth are summarized in Table 2. The addition of Co resulted in increases in the fresh and dry weights and in the chlorophyll and total N contents of tops of plants. The differences in most cases were striking. The effect of Co on the growth of the plants (as illustrated by the photograph in Figure 2), was consistent in all replicates.

The responses to the Co treatments in the final harvest were less striking than those observed in the previous harvest (Tables 3 and 4). Still the Co addition resulted in a marked increase in the dry weight and in the total N content in roots (Table 4). Even though the Co treatment resulted in increases in many of the determinations (Tables 3 and 4), the variation between replicates was so great that many of the differences were not statistically significant. The lack of response to Co in the final harvest may be attributed to the fact that cultures were exposed to greenhouse contamination for a long period of time. Plants apparently obtained adequate Co from nutrient solutions and other sources to meet their needs.

Additional replications and more refined methods will be necessary to study in detail the Co requirements for the growth of this species.

TABLE 2. Effect of cobalt treatment on the growth and composition of alder plants[1]
(First harvest – age 144 days)

Treatment (ppb)	Height	Fresh weight of tops	Dry weight of tops	Chloro- phyll in fresh leaves	Nitrogen in tops	Nitrogen in tops
	Cm	*Grams per culture*	*Grams per culture*	*Mg/g*	*Percent of dry matter*	*Mg per culture*
Cobalt, 0	19.5	8.6	1.9	1.72	2.67	50.7
Cobalt, 50	31.5	41.6	9.8	3.12	2.66	260.7
Differences significant at probabilities of:	10%	5%	5%	1%	NS	5%

[1]*Data reported are means of measurements on four replicate cultures.*

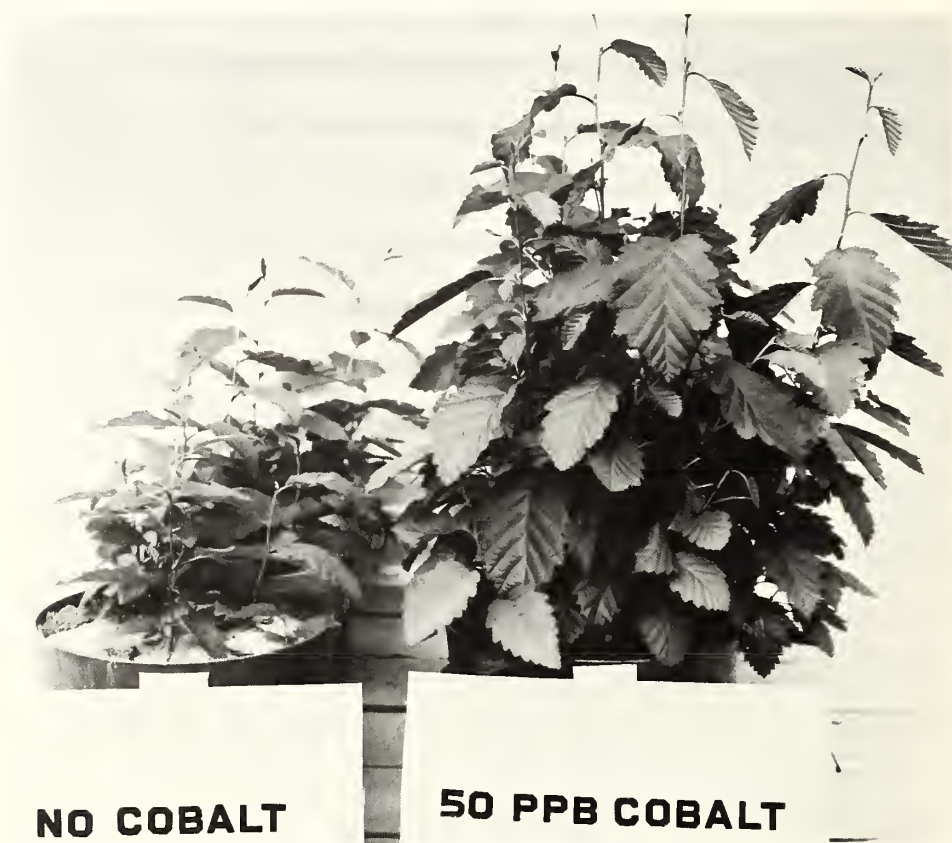**NO COBALT**   **50 PPB COBALT**

Figure 2. An illustration of the effect of Co on the growth of *Alnus rubra*. Cultures were provided with a complete nutrient solution with the exception that Co was omitted or 50 ppb (0.05 ppm) were added as indicated. Plants were 144 days old when the photograph was made.

TABLE 3. Effect of cobalt treatment on the growth and composition of alder plants[1]
(Final harvest — age 213 days)

Treatment (ppb)	Height	Fresh weight of tops	Dry weight of tops	Chloro-phyll in fresh leaves	Nitrogen in tops	Nitrogen in tops
	Cm	*Grams per culture*	*Grams per culture*	*Mg/g*	*Percent of dry matter*	*Mg per culture*
Cobalt, 0	47	70.8	19.2	3.31	2.00	384
Cobalt, 50	46	93.9	27.5	3.23	1.87	514
Differences significant at probabilities of:	NS	NS	NS	NS	NS	NS

[1] *Data reported are means of measurements on four replicate cultures.*

Effects of Trace Metals on the Vitamin B_{12} Content of Nodules

Increasing concentrations of Ni, Fe, and Mn in nutrient solutions strikingly influenced the vitamin B_{12} content of alder nodules (Fig. 3, A, B, C). The effect of increasing concentrations of Ni were most pronounced (Fig. 3A). Nodules from plants grown without Ni and with 0.05 ppm Co contained about 130 mμg of vitamin B_{12} per g of fresh nodules. In comparison,

TABLE 4. Effect of cobalt treatment on the growth and composition of alder roots and nodules[1]
(Final harvest — age 213 days)

Treatment (ppb)	Fresh weight of roots	Dry weight of roots	Nitrogen in roots	Nitrogen in roots	Nitrogen in whole plants	Fresh weight of nodules
	Grams per culture	*Grams per culture*	*Percent of dry matter*	*Mg per culture*	*Mg per culture*	*Grams per culture*
Cobalt, 0	39.9	6.2	0.98	60.7	445	4.6
Cobalt, 50	56.1	15.6	1.07	166.9	681	6.9
Differences significant at probabilities of:	NS	10%	NS	10%	NS	NS

[1] *Data reported are means of measurements on four replicate cultures.*
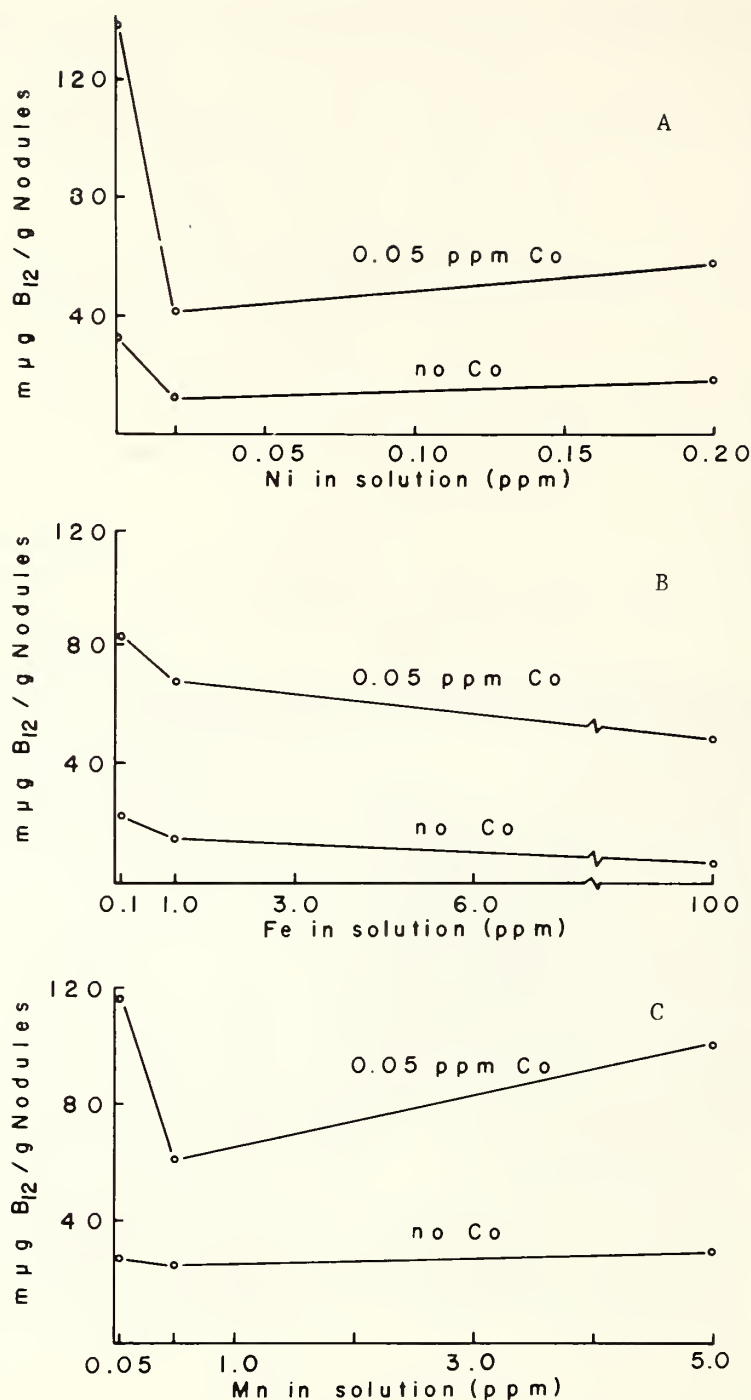
Figure 3.   The effect of increasing Ni, Fe, and Mn in nutrient solutions on the vitamin B_{12} content of nodules of *Alnus rubra*. *A*, The vitamin B_{12} content of fresh nodules of *A. rubra* as influenced by Ni as $NiCl_2$ content in the nutrient solutions; *B*, the influence of increasing Fe, as FeEDDHA in nutrient solutions on the vitamin B_{12} content of fresh nodules from *A. rubra*; *C*, the effects of increasing concentrations of Mn as $MnCl_2$ in the nutrient solution on the vitamin B_{12} content in fresh nodules from *A. rubra*.

nodules from plants grown without added Ni and Co contained only about 32 m μ g B_{12} per g of fresh nodules. The addition of 0.02 ppm Ni to cultures with or without added Co resulted in a sharp decline in the B_{12} content of nodules. The effect was most striking, however, when the higher (0.05 ppm) Co level was supplied. As shown by the curves in Figure 3A, the addition of 0.2 ppm Ni to cultures supplied with 0.05 ppm Co resulted in a slight increase in the B_{12} content of nodules as compared to the effect of the addition of 0.02 ppm Ni to comparable cultures (Fig. 3). The increase in B_{12} content associated with an increasing concentration of Ni may be attributed to Co contamination in the Ni salts. An analysis of the $NiCl_2$ revealed a Co content of 420 μ g/g of $NiCl_2$.

The effect of increasing the Fe content of the nutrient solution on the amount of vitamin B_{12} in nodules exhibits trends similar to those obtained with increasing Ni in nutrient solutions. The B_{12} content of nodules from cultures supplied with 0.05 ppm Co and 0.1 ppm Fe was 84 m μ g/g (Fig. 3B). In contrast, nodules from cultures with 0.1 ppm Fe but no added Co contained about 22 m μ g of B_{12} per g. An increase in Fe concentration in nutrient solutions from 0.1 to 0.5 ppm resulted in a sharp decrease in the vitamin B_{12} content of nodules, but the effect of further addition of Fe (100 ppm) was less dramatic. The slight increase in B_{12} resulting from a supply of 100 ppm Fe also may be attributed to Co contamination in the Fe source. Analysis showed that the FeEDDHA contained 19 μ g Co per g.

Increasing the concentrations of Mn in nutrient solutions results in a pattern of vitamin B_{12} contents of nodules with trends similar to those observed by increasing concentrations of Ni and Fe in nutrient solutions (Fig. 3C). Nodules from cultures treated with 0.05 ppm Co and 0.05 ppm Mn contained about 115 m μ g of B_{12} per g. As the Mn concentration was increased in the nutrient solution with 0.05 ppm Co, there was a marked decrease in vitamin B_{12} content of nodules to a concentration of about 60 m μ g per g. Further addition of Mn (5 ppm) was associated with an increased B_{12} content of nodules to about 100 m μ g per g. This increase may be attributed to Co contamination of 7 μ g per g of $MnCl_2$.

In general, the results obtained from adding increasing concentrations of Mn in the nutrient solutions on the B_{12} content of nodules supports the hypothesis that excesses of these trace elements compete with Co in the synthesis of B_{12} compounds. The results are complicated to some extent by the fact that all three of the trace elements added contained appreciable Co impurities.

The Effect of Trace Metals on the Cobalt Content of Alder Tops and Roots

Since the results of vitamin B_{12} analysis indicated that increasing concentrations of Ni, Mn, and Fe influenced the content of vitamin B_{12} in nodules, it was of interest to determine whether increasing concentrations of these transition metals affected the Co content of the plant material. The Co content of dry alder tops from cultures supplied with nutrient solutions lacking added Co increased slightly with increasing amounts of Ni in the nutrient solution (Fig. 4A). In contrast, the Co content of dry plant material

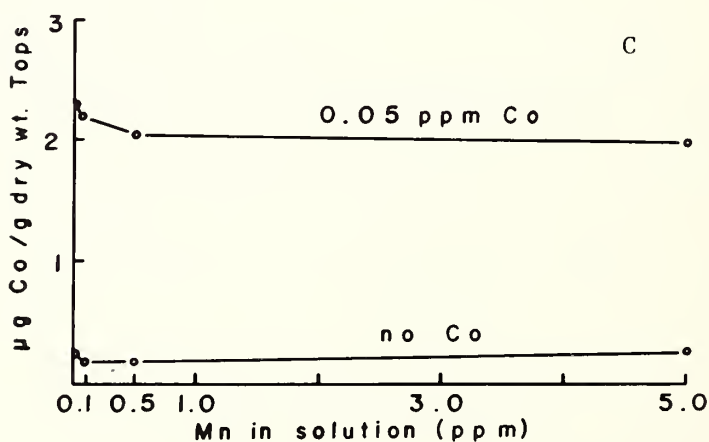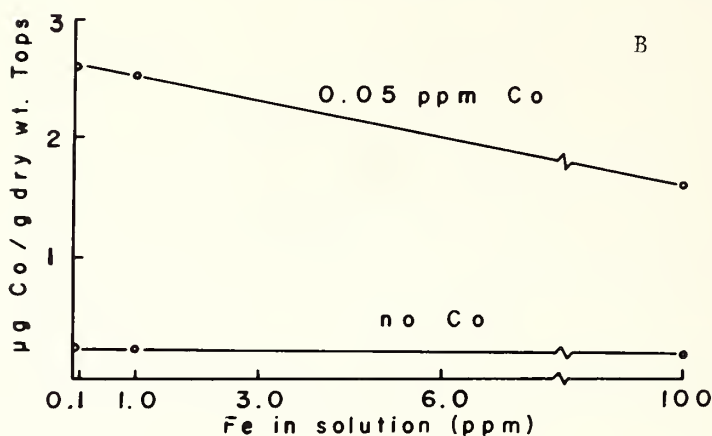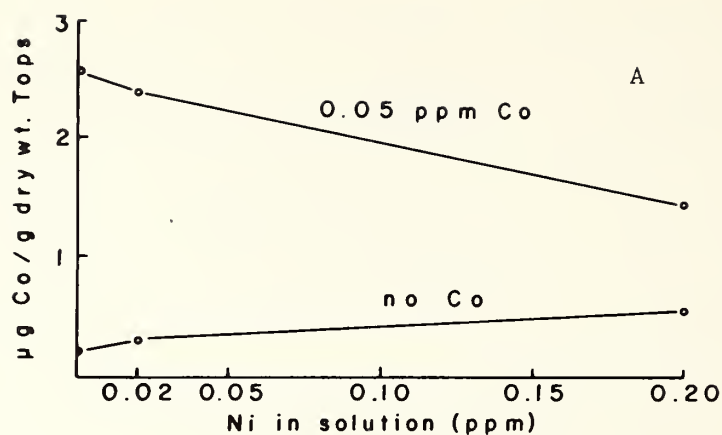Figure 4.   The effects of Ni, Fe, and Mn on the Co content of tops of *Alnus rubra. A,*
The Co content of tops of *A. rubra* as influenced by increasing concentrations
of Ni as NiCl$_2$ in nutrient solutions; *B,* the effects of increasing concentrations
of Fe as FeEDDHA on the Co content of tops of *A. rubra; C,* the influence
of different concentrations of Mn as MnCl$_2$ on the Co content of tops of
A. rubra.

from cultures supplied with 0.05 ppm Co decreased from about 2.6 μg per g where no Ni was added to the solution to about 1.5 μg per g where 0.2 ppm Ni was added to the solution.

Similar trends are presented in Figure 4B. Where no added Co was supplied to the nutrient solutions, the addition of increasing concentrations of Fe in the solution had little effect on the Co content of the plant material. The material from cultures supplied with 0.05 ppm Co in the nutrient solution showed a marked decrease in Co content as the level of Fe was increased from 0.1 ppm to 100 ppm Fe in the nutrient solution.

In Figure 4C it is apparent that the addition of increasing concentrations of Mn in the nutrient solution had little effect on the Co content of tissues from cultures lacking added Co in the nutrient medium. Plants from cultures supplied with 0.05 ppm Co in the solution showed a slight decrease in Co content as Mn was increased from 0.05 ppm to 5 ppm. In general, these results indicate that increasing concentrations of either Ni, Fe, and to some extent Mn were associated with a decreased Co content of the plant material. The effects may be attributed to some type of competition among trace metals in the process of Co utilization or uptake.

In Figure 5A, 5B, and 5C the influences of different concentrations of Ni, Fe, and Mn in nutrient solutions on the Co content of alder roots is presented. The addition of increasing concentrations of Ni, Fe, or Mn to cultures supplied with either 0.05 ppm Co or no added cobalt generally caused a decreased Co content.

It appears that the effect of the addition of excessive concentrations of trace elements on Co uptake of alder plants is consistent with the results showing that the increasing concentrations of these trace elements interfere with the biosynthesis of vitamin B_{12}. In regard to uptake, the effects of elements are less striking than the effects of excessive trace elements on B_{12} biosynthesis. It is suggested, therefore, that the content of vitamin B_{12} in alder nodules may provide a better index of biologically functional Co than the Co content of tissues.

These results also suggest that the adequacy of Co supply in soils or artificial nutrient media for nitrogen fixation of symbiotic may be influenced, not only by the amount Co available for the plants but also by the concentration of other transition elements in growth media that may compete with Co in those metabolic processes in which Co participates.

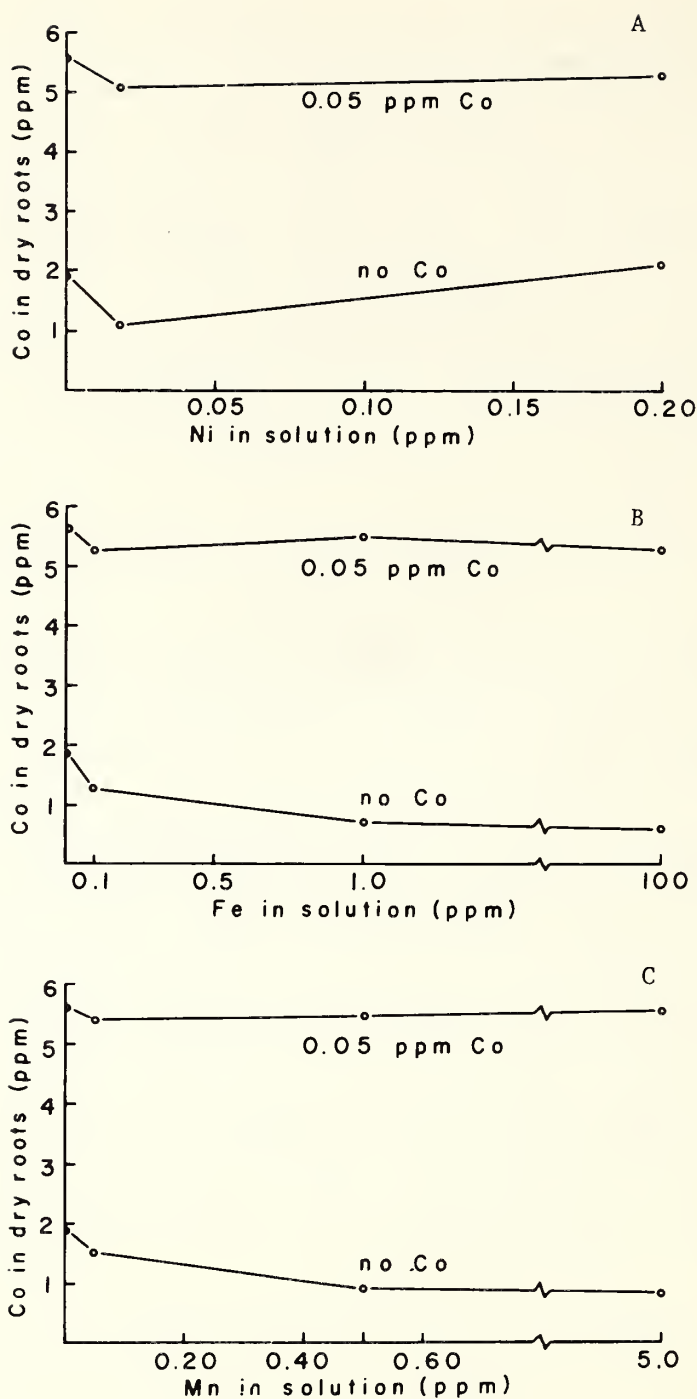Figure 5.   The effects of Ni, Fe, and Mn in nutrient solutions on the Co content of roots of *Alnus rubra*. *A,* The Co content of roots of *A. rubra* as influenced by increasing concentrations of Ni as NiCl$_2$; *B,* the effects of increasing concentrations of Fe as FeEDDHA on the Co contents of roots of *A. rubra; C,* the influence of increasing concentrations of Mn as MnCl$_2$ on the Co content of roots of *A. rubra.*

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Growth and yield of red alder in British Columbia

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Abstract

A gross volume of 1 billion cubic feet of red alder exists on about 350,000 acres of British Columbia forest land that could produce much higher values if stocked with Douglas-fir or black cottonwood. However, the characteristically rapid juvenile growth of alder from seed, which permits full stocking at early ages, may prove valuable for management of alder on very short rotations. Data are presented on radial growth and important tree characteristics for open- and forest-grown trees. Regressions of crown width on dbh and a yield table based on these are included. It is shown that crown width and root spread are highly correlated. Several total cubic-foot tree volume equations are given, and it is noted that one of these, V/B = 0.44H, also can be used to estimate growth and yield per acre. Merchantable volume factors and reductions for decay, waste, and breakage are summarized. Distributions of section volumes and diameters inside bark are described by regression equations. Data on bark thickness and percentage are summarized. British Columbia Forest Service normal yield and stand tables for alder and Schon's empirical merchantable yield table, as well as data from University of British Columbia campus and Haney Forests, are used to illustrate the need for early and effective control of spacing.

Introduction[1]

Although red alder (*Alnus rubra* Bong.) is of only minor commercial interest in British Columbia, some information on biological and other aspects of growth is accumulating. Hardwoods occupy only 0.1 percent of the mature forest area but 5 percent of the immature area, a relative increase of 50 times. On more than 200,000 acres of land on the south coast of British Columbia, capable of growing excellent Douglas-fir, the predominant species is alder, often low in quality and of limited commercial value (Ker,

[1]*Abbreviations used in this paper: Ccf, 100 cu. ft.; dbh, diameter breast height; B. C., British Columbia; fbm, board feet; CW, crown width; D, diameter breast height; SE_E, standard error of estimate; r^2, coefficient of determination; r, correlation coefficient; V, total cubic-foot volume inside bark; H, total height in feet; B, square feet of basal area outside bark, measured at breast height; Vs, sectional total cubic-foot volume to any given height; h, any given height; dib, diameter inside bark; d, diameter inside bark; bt, bark thickness; dbt, double bark thickness; dob, diameter outside bark; dbhob, diameter breast height outside bark; Vg, volume growth; Hg, height growth; LC, live crown; SD, standard deviation; R, radial growth; Dhm, diameter at height of measurement.*

Smith, and Little, 1960). Concern for control of alder has been expressed colorfully by Dr. V. J. Krajina of the University of British Columbia, Department of Biology and Botany. He has likened the spread of alder on lands more valuable for growing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to an epidemic of trees requiring prompt and effective control.

There is little doubt that growth of Douglas-fir greatly exceeds that of alder in both volume and value (Dobie, 1966). Maximum conversion return (margin for stumpage profit and risk) for alder lumber might be $6 per hundred cubic feet (Ccf) (Tessier and Smith, 1961) but $35 per Ccf for Douglas-fir on the same site (Dobie, 1966). Black cottonwood (*Populus trichocarpa* Torrey and Gray)(Smith, 1957a) also consistently outproduces alder but requires more intensive management (Smith and Blom, 1966).

Inventory

Rymer (1951) noted that until 1930 alder was regarded more or less as a weed species and was not recorded by timber cruisers.

Alder represented only about 0.2 percent of the gross volumes of wood inventoried by the British Columbia Forest Service in all British Columbia forests as of 1957, yet its gross volume of 1 billion cubic feet forms a potentially valuable resource. As of 1957, there was an estimated 606 million cubic feet of sound wood in alder trees 10 inches dbh and over on the coast and 46 million cubic feet in the interior of British Columbia. Use of alder for lumber in British Columbia increased from 680,000 fbm in 1934 to 7.2 million fbm in 1946 (Wellwood, 1956) but has declined gradually since then. The annual report of the British Columbia Forest Service showed that less than 5 million fbm of alder were cut in 1965.

In 1957 on the British Columbia coast, there were 92,044 acres of young, immature red alder stands. Since the total area of all stands classed as pure alder type was only 106,797 acres, it is reasonable to expect alder to increase in importance as the young stands mature. Moreover, it is a component of at least 250 thousand acres of mixtures with other deciduous species and conifers.

Succession

Because red alder is relatively short lived, it is possible to rely on natural succession to convert alder stands to more valuable conifers. We have seen this take place in stands following wildfire in 1868 and logging in the 1920's on the University of British Columbia Research Forest north of Haney. Comparison of aerial photos taken in 1930 with 1960 and subsequent series has provided data on stand development and deterioration (Smith, 1957b; Wang, 1965). Between 1949 and 1955, red alder became much less noticeable. In 1965, very few alder trees could be seen and their place was taken by conifers in aerial photographs of stands which had appeared as nearly pure alder in 1949.

Schon (1960) observed that by 50 years most alder stands on Douglas-fir site IV (alder 57 feet at 50 years) are breaking up. Many show dieback and

other symptoms of old age as early as age 40. The same fate awaits alder on site III (alder 73 feet at 50 years) at or near age 60. Alders on site II (alder 90 feet at 50 years) begin to deteriorate at 70 years of age, and few stands remain intact beyond 100 years.

Alders averaged 43 years in age on the area studied by Tessier and Smith (1961) which had been burned in 1868. Therefore, these trees must have been a second generation following the original disturbance. Their ages ranged from 25 to 56 years on two 5-acre blocks. The largest alder was 32 inches in dbh, much smaller than the best Douglas-fir which was 44 inches in dbh and 193 feet tall at age 78.

Stand Formation

Because it usually needs bare mineral soil or moist humus free of competition to establish itself, red alder often is so poorly distributed that it fails to occupy the site fully. Few alder plots in 20- to 60-year-old stands on the University of British Columbia Research Forest supported more than 100 square feet of basal area per acre. Yet stands following clearing of 200 acres of the University of British Columbia endowment lands in 1953 averaged 60 square feet of basal area per acre at stand age 10, and at extreme stand densities carried as much as 280 square feet of basal area per acre. Alder will tolerate high stand densities when very young. I have counted 150 alder stems per milacre at age 1 and 40 stems per milacre at age 2 in stands established on bare mineral soil. Such high densities and rapid height increment can lead to growth of as much as 40 square feet of basal area per acre in 1 year.

Tree Development

RADIAL GROWTH

Apsey (1961) measured radial growth and other characteristics of 72 open-grown and 50 forest-grown red alders near Haney, Whiterock and Vancouver. These are summarized in Table 1. Radial growth was highly variable but significantly associated with dbh, total height, age, height to live crown, bark thickness, and crown width. Although radial growth could be predicted with statistically significant regression equations, their practical importance was diminished greatly by their large standard errors of estimate.

HEIGHT GROWTH

On good sites, very young alder commonly grows 5 feet annually. Apsey (1961), who measured 100 young dominant and superdominant alder, found that alder took only 1 year to reach breast height on good sites, and 2 years were required for medium and 3 for poor sites (respectively, 112, 96, and 80 feet at age 50). In 1963, J. Walters cut an alder, from plantation No. 9 on the University of British Columbia Research Forest, that was 32.1 ft tall and 6.4 in. in dbh at the end of its 5th year from seed. Its annual height increments from seed were: 7.9, 6.5, 5.6, 6.4, and 5.7 ft.

TABLE 1. Summary of statistics of basic data for 72 open-grown and 50 dense-grown red alder (Apsey, 1961)

Variable	Unit	Open-grown		Dense-grown	
		Mean	SD	Mean	SD
dbh	in.	11.4	5.28	10.3	3.52
Form		.886	.14	.944	.04
Height	ft	53	20.15	71	18.84
H to LC	ft	13	11.04	39	15.74
Live crown (LC)	%	77.0	.11	45.7	.12
Age	years	24	10.61	30	12.54
Site index	ft	78	15.88	95	15.41
Bark thickness	in	.20	.11	.17	.07
R1-5	in	.73	.40	.48	.29
R6-10	in	.84	.45	.48	.31
CW/dbh	ft /in.	2.43	.59	1.61	.36
CW	ft	26	8.80	16	5.05

Form is dob at 9 ft /dbhob. Site index is estimated total height at age 50. R is radial growth of wood 1 to 5 or 6 to 10 years ago (1956-60 or 1951-55). CW is crown width, the average of two diameters, one measured at the widest portion of the crown and the other at right angles to this. SD is standard deviation.

CROWN WIDTH

Apsey (1961) found that the regression of crown width (CW) in feet of 72 open-grown trees on dbh (D) in inches was significantly different from that for 50 forest-grown trees.

$$\text{Open CW} = 8.032 + 1.530 \, D, \quad SE_E = 3.47 \text{ ft}, \quad r^2 = 0.846$$
$$\text{Forest CW} = 3.843 + 1.174 \, D, \quad SE_E = 2.93 \text{ ft}, \quad r^2 = 0.669$$

Both of these equations should be revised to estimate CW of very young trees, which have CW of only 2 to 4 feet when they reach 4.5 feet in height.

These do not support the view of Worthington, Ruth, and Matson (1962) that "alder occupies two or three times more growing space per tree than native conifers. This is due to its wider crown and intolerance to shade." Open-grown Douglas-fir and alder have similarly wide crowns, but forest-grown Douglas-fir crowns are smaller than those of alder for the same dbh (Smith, 1966).

ROOT SPREAD

Branch length and root spread of 33 red alders are significantly correlated (r^2=0.518) (Smith, 1964). The median number of primary roots was 8, the median ratio of the longest root to the average root was 1.2, median rooting depth was shallow (1.5 feet), and no tree roots penetrated deeper than 4 feet. Since only 19.5 percent of the zone marked by lateral roots was effectively occupied, it appears likely that crown competition is more limiting to growth than is root competition.

VOLUMES PER TREE

It now is conventional in British Columbia to use total cubic-foot volumes inside bark (V), based on dbh (D) in inches and total height (H) in feet, with appropriate reduction factors to allow for degree of utilization, waste, breakage, and decay. Utility of equations can be compared by standard error of estimate (SE_E) and coefficient of determination (R^2 or r^2).

The first standard total cubic-foot volume tables of the British Columbia Forest Service for alder based on 258 trees used the equation:

$\log V = -2.68495 + 1.92813 \log D + 1.07851 \log H$, $SE_E = \pm 10.0\%$, 0.46% low.

Their second standard total cubic-foot volume table (Browne, 1962) based on 599 trees was better. It used the equation:

$\log V = -2.672775 + 1.920617 \log D + 1.074024 \log H$, $SE_E = \pm 8.3\%$, 0.24% high.

This second table was simplified by Smith and Breadon (1964) who showed that $V = 0.02 + 0.246 \frac{D^2 H}{100}$ up to $\frac{D^2 H}{100}$ of 60.

For larger trees $V = 1.85 + 0.228 \frac{D^2 H}{100}$. These combined variable equations can be transformed to estimate the ratio of V to basal area (B) outside bark at 4.5 feet in square feet. For small trees $V/B = \frac{3.67}{D^2} + 0.451\ H$. For larger trees $V/B = \frac{367}{D^2} + 0.418$. The equations represented trees 2 to 22 inches in dbh.

By direct transformation of combined variable equations Smith and Munro (1965) found that since $V = 0.02 + 0.242 \frac{D^2 H}{100}$ for all alder trees, V/B equaled 0.44H.

Smith and Munro (1965) also analyzed data on 101 alders provided by the British Columbia Forest Service which averaged 12.7 inches dbh and ranged from 5 to 30 inches. Heights averaged 83.2 feet and ranged from 53 to 108 feet (Kozak and Smith, 1966). They found that $V/B = 2.2208 + 0.4229H$ with an SE_E of 3.32 and r^2 of 0.68.

Munro (1967) tabulated ratios of standard cubic-foot volume to basal area for the commercial tree species of British Columbia using Browne's (1962) equations.

Merchantable volume factors from Browne (1962) are shown in Table 2. Net volume (loss) factors for decay, waste, and breakage based on 375 trees were published by the British Columbia Forest Service in their Forest Survey Note No. 8 (1966). These show no decay for trees up to 40 years of age and only 8 percent breakage in trees 9.1 inches and larger in dbh (factor 0.92). Reductions of from 1 to 7 percent must be made for decay in trees over 40 years in age. The combined factor for decay, waste, and breakage in trees 11.1 inches and larger without visible indicators of decay is 0.920, and for trees with visible indicators of decay it is 0.820.

Use of total cubic-foot volumes with appropriate reduction and conversion factors is a very flexible method of providing total information about utilization possibilities to any desired standard.

TABLE 2. Merchantable volume factors for red alder (Browne, 1962)

Dbh class	Close utilization	Intermediate utilization	Rough utilization
2			
4	0.38		
6	.82		
8	.90	0.16	
10	.94	.58	
12	.95	.75	0.03
14	.95	.83	.36
16	.96	.88	.60
18	.96	.90	.72
20	.96	.91	.75
22	.96	.91	.75
24	.96	.91	.75
26	.96	.91	.75
28	.96	.91	.75
30	.96	.91	.75

Factor X total volume of entire stem equals merchantable volume to stump and top limits shown.
Close utilization: Stump height of 1 ft, top dib of 4 in.
Intermediate utilization: Stump height of 1.5 ft, top dib of 8 in.
Rough utilization: Stump height of 2 ft, top dib of 12 in.

FORM

Estimation of sectional total cubic-foot volume (Vs) to any height (h) within trees of total height (H), dbh (D), and total cubic-foot volume (V) was studied by Smith and Munro (1965) and Kozak and Smith (1966). For 101 alder trees 53 to 108 feet in height:

$$V_S/V = 0.018 - 1.111 \ h^2/H^2 + 2.085 \ h/H, \ SE_E = 0.025, \ r^2 = 0.994.$$

Estimation of dib (d) at any section height (h) can be made by use of the equation calculated recently by Dr. A. Kozak for the same red alders:

$$d = D\sqrt{1.08862 - 1.62051 \ h/H + 0.53189 \ h^2/H^2}$$

This equation estimated dib at each of 11 sections for the 101 trees with a standard error of estimate of 0.75 inch. It had very little error in the lower 40 percent of the tree, and individual section deviations from it appeared to be random.

BARK

Apsey (1961) observed that equations for estimation of single bark thickness at breast height were significantly different for his open- and forest-

grown groups of trees. bt = - 0.0630 + 0.019 dbh with SE_E = 0.032 for dense, and - 0.0111 + 0.0184 dbh with SE_E = 0.045 for open-grown trees.

Smith and Kozak (1967) observed that age (r = .55) and dbh (r = .51) were the best indicators of alder double bark thickness (dbt) at breast height. Dbt at tenths of total height above breast height could be estimated best from section dob (r = .72) and dbt at breast height (r = .74). Dbt of 946 sections averaged 0.50 inch and ranged from 0.01 to 1.3 inches. Dbt as a percentage of dob averaged 7.0 and ranged from 2.6 to 40.0 percent. Double bark thickness at breast height averaged 0.6 inch for 86 trees and ranged from 0.2 to 1.0 inch. Percentage dbt at breast height averaged 5.3 and ranged from 2.6 to 9.1 percent. Percentage dbt of 28 roots averaged 11.5 percent. For 33 root collar bark thicknesses the average was 4.7 percent; branch butt bark thicknesses averaged 10.7 percent; and branch middle bark thicknesses averaged 9.2 percent.

For 946 sections dbt = - 0.052 + 0.058 dob + 0.002 h/H with an SE_E = .148 and r^2 = 0.558. Dbt also can be estimated from 0.21 + 0.041 dbh - 0.348 h/H with SE_E = 0.163 and r^2 = 0.465.

Stand Growth and Yield
YIELD

The British Columbia Forest Service yield tables, published in 1938 for well-stocked red alder stands, are given as Table 3. Their average diameter stand tables are included as Table 4 and Schon's (1960) empirical yield tables are reproduced as Table 5. For the 1957 and subsequent inventories, yields of alder in British Columbia have been lumped by the British Columbia Forest Service with other species under a general heading of "deciduous" species.

Apsey (1961) used data on crown widths to prepare a yield table for open and dense stands which is shown herein as Table 6. Tables 3 to 6 provide a useful supplement to the normal yield table prepared by Worthington et al. (1960).

As mentioned earlier, volumes per acre can be estimated easily during cruising by using the appropriate point sampling factor (Smith and Munro, 1965). For example, yield per acre in total cubic feet will equal B x 0.44H for alder.

Warrack (1949, 1958) has studied thinning of alder. As in most other species, early control of spacing is highly desirable (Smith, 1966) but is difficult to justify economically for alder.

DEFINING GROWTH AND YIELD
WITH THE TREE VOLUME EQUATION

The tree volume equation V/B = 0.44H also can be used to establish some general limits for definition of stand growth and yield. It can be redefined to give volume per acre in terms of basal area per acre and average stand height. Also, if site quality is defined in terms of average annual height growth and if basal area per acre is specified or is estimated by point sampling, both annual

TABLE 3. Normal yield table for red alder (B.C. Forest Service, 1938)

Age (years)	Average dbh	Average height dominant and dominant	Trees per acre (1 in. and over)	Volume per acre	
				Trees 1 in. and over	Trees 6.6 in. and over
	Inches	*Feet*	*Number*	*Cubic feet*	*Board feet*

Site index 112 (good) (Site indices 105 to 130 at 50 years)

Age	dbh	height	trees	cubic	board
10	3.6	55	1,300	2,100	-
15	5.2	66	700	2,850	1,000
20	6.7	76	460	3,500	7,000
25	8.0	85	335	4,150	12,250
30	9.3	92	260	4,680	17,250
35	10.4	98	210	5,125	21,750
40	11.6	104	175	5,550	26,250
45	12.7	108	152	5,975	30,500
50	13.6	112	135	6,310	33,500
55	14.4	115	122	6,650	37,000
60	14.9	118	118	6,970	38,250

Site index 96 (medium) (Site indices 85 to 104 at 50 years)

Age	dbh	height	trees	cubic	board
10	3.1	43	1,600	1,520	-
15	4.5	53	890	2,205	-
20	5.9	63	560	2,850	3,400
25	7.2	71	400	3,450	7,800
30	8.5	77	305	3,950	12,750
35	9.6	83	245	4,350	18,500
40	10.6	88	205	4,675	23,500
45	11.5	93	180	4,975	27,600
50	12.2	96	160	5,200	30,750
55	12.8	99	145	5,425	33,150
60	13.2	101	140	5,600	35,000

Site index 80 (poor) (Site indices 70 to 84 at 50 years)

Age	dbh	height	trees	cubic	board
10	2.4	32	2,200	820	-
15	3.8	42	1,100	1,350	-
20	5.2	50	700	1,850	-
25	6.5	56	485	2,340	1,000
30	7.7	63	360	2,800	5,040
35	8.6	68	300	3,230	9,450
40	9.5	73	250	3,650	14,500
45	10.2	77	220	4,000	19,360
50	10.8	80	195	4,256	21,060
55	11.4	83	180	4,450	23,940
60	11.8	85	170	4,590	26,690

Yield table for well-stocked stands. Site index based on average height of dominant and codominant trees at 50 years. Cubic volume is based on trees 1 inch and larger. Board-foot volume is based on trees 6.6 inches and larger scaled in 8-ft sections, B.C. rule, to an average top diameter of 8 inches ob.

TABLE 4. Stand table for red alder. Based on mean diameter[1] of stand and expressed by diameter classes in percent of total number of trees.

Dbh class (inches)	Mean diameter of the stand (inches)											
	2	3	4	5	6	7	8	9	10	11	12	13
	Proportion of trees found in each diameter class of the stand in percent											
1	34.0	17.8	5.2	4.5	-	-	-	-	-	-	-	-
2	37.5	23.0	15.2	11.0	1.0	0.5	-	-	-	-	-	-
3	22.0	26.1	22.5	15.0	7.2	2.5	1.5	1.0	-	-	-	-
4	6.0	20.0	25.2	18.0	13.0	7.5	6.0	3.5	0.5	-	-	-
5	.5	9.0	20.0	19.5	18.7	13.0	10.8	5.8	2.8	1.5	1.0	0.3
6	-	4.0	8.6	15.2	21.4	17.0	13.5	8.2	6.0	3.5	3.0	1.5
7	-	.1	3.1	10.1	18.7	20.0	15.4	10.5	9.0	5.6	5.5	2.8
8	-	-	.2	5.6	12.0	15.8	16.5	13.0	11.7	8.0	7.6	4.2
9	-	-	-	1.1	6.0	10.5	14.5	14.5	14.4	10.7	10.0	5.5
10	-	-	-	-	1.5	7.0	10.0	13.0	15.8	13.0	12.4	7.0
11	-	-	-	-	.5	4.1	5.8	10.5	13.9	14.5	13.5	8.9
12	-	-	-	-	-	1.8	3.4	8.3	10.7	13.2	13.5	10.7
13	-	-	-	-	-	.3	2.0	6.0	7.2	11.0	12.0	12.0
14	-	-	-	-	-	-	.6	3.8	4.7	8.5	10.0	11.7
15	-	-	-	-	-	-	-	1.5	2.5	5.8	6.5	10.5
16	-	-	-	-	-	-	-	.4	.8	3.3	3.0	8.4
17	-	-	-	-	-	-	-	-	-	1.2	1.5	6.5
18	-	-	-	-	-	-	-	-	-	.2	.5	4.7
19	-	-	-	-	-	-	-	-	-	-	-	3.2
20	-	-	-	-	-	-	-	-	-	-	-	1.6
21	-	-	-	-	-	-	-	-	-	-	-	.5
Sum	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[1]*Arithmetic mean of diameters (not the diameter of average basal area).*
Compiled by H. G. McWilliams, 1938, for B. C. Forest Service.

growth and total yield can be found simply and with sufficient accuracy for many purposes (Smith, 1967).

If annual alder Vg is 100 cubic feet per acre and annual Hg is 5 feet, then $100 = B \times 0.44 \times 5$ and $B = 45.4$ square feet. This means that stand density must be:

> 45.4 trees, 13.5 inches in dbh (B = 1 ft.)
> or 454 trees, 4.5 inches in dbh (B = 0.1 ft.)
> or 4540 trees, 1.4 inches in dbh (B = 0.01 ft.)

To grow 300 cubic feet per acre annually, stand density must be 3 x 45.4 or 136.2 square feet of basal area with an annual height growth of 5 feet.

TABLE 5. Empirical merchantable yield table, alder, Powell River, 1956[1]

Age (years)	Volume per acre	Trees per acre 5 in. and larger[2]	Average total height[3]	Average basal area per acre	Average dbh
	Cubic feet	Number	Feet	Square feet	Inches
Douglas-fir site II (170 feet at 100 years)					
10	-	-	36	16	-
15	-	-	49	44	-
20	2720	180	60	78	8.9
25	3700	250	69	107	8.8
30	4380	270	76	121	9.1
35	4770	258	80	130	9.6
40	4980	242	84	136	10.1
45	5100	218	87	138	10.8
50	5160	195	90	139	11.4
55	5200	170	93	138	12.2
60	-	142	95	134	13.1
Douglas-fir site III (140 feet at 100 years)					
10	-	-	33	14	-
15	-	-	44	27	-
20	1440	228	53	53	5.4
25	2350	252	59	76	7.4
30	2650	248	64	91	8.2
35	2750	235	67	102	8.9
40	2800	220	70	106	9.4
45	2830	203	72	109	9.9
50	2850	186	73	108	10.3
55	-	166	-	-	-
Douglas-fir site IV (110 feet at 100 years)					
10	-	-	28	8	-
15	-	-	38	18	-
20	920	212	45	30	6.1
25	1380	218	50	48	6.3
30	1560	214	52	66	7.5
35	1620	206	54	80	8.4
40	1660	198	55	88	9.0
45	1680	188	56	90	9.3
50	-	177	-	-	-
55	-	166	-	-	-

[1] Source: Schon (1960).
[2] Basis: 408 0.025-acre temporary plots. Cubic-foot volumes of all alder 5 inches and larger in dbh to a 4-inch top; stump height, as cut.
[3] Average height of dominants and codominants.

TABLE 6. Yield table for red alder based on crown width (Apsey, 1961) for open-grown and forest or dense-grown stands

Average dbh (inches)	Curved height		Volume per tree		Trees per acre		Volume per acre	
	Open grown[1]	Dense grown[2]	Open grown	Dense grown	Open grown	Dense grown	Open grown	Dense grown
	Feet		*Cubic feet*		*Number*		*Cubic feet*	
4	24.5	39.3	1.0	1.6	222	538	222	861
6	33.6	53.1	3.0	4.8	151	360	452	1,728
8	42.1	64.5	6.8	10.4	109	258	741	2,683
10	49.9	73.4	13.1	18.6	82	170	1,074	3,162
12	57.1	79.9	20.7	28.3	64	135	1,325	3,820
14	63.7	84.0	30.6	39.9	52	109	1,591	4,349
16	69.6	85.6	43.0	52.6	42	83	1,806	4,366
18	75.0		58.1		34	70	1,975	
20	79.7		75.8		29	60	2,198	
22	83.8		96.0		25	48	2,400	
24	87.2		118.5		22	43	2,607	
26	90.1		143.4		19	38	2,725	

[1] $H = 4.5 + 5.32\ (dbh) - .078\ (dbh^2)$, H max. 95.2 feet, Dhm 34.1 inches
[2] $H = 4.5 + 9.92\ (dbh) - .303\ (dbh^2)$, H max. 85.7 feet, Dhm 16.4 inches

The general equation can be manipulated to illustrate any desired combination of B and H required to utilize an annual growth capacity of V.

Data from 32 point samples on the University of British Columbia endowment lands show that alder basal area has built up at a rate of about 2.5 square feet per foot of average tree height, or about 5 square feet of basal area per acre per year from seed. Average annual height growth of alder on these lands averages about 2.5 feet and ranges from 1.2 to 4.2 feet.

Future Possibilities for Alder in British Columbia

Because alder can be established easily by seeding on well-disturbed land, a very large number of fast-growing alder trees could grow quickly to a high level of basal area per acre. These might be managed similarly to the "silage" sycamore of McAlpine et al. (1966) who are optimistic about growing hardwood pulpwood trees on 2- to 3-year rotations.

It may even be that alder will find its best use as silage which can be stored on the stump and harvested as required, if the experiments of Dr. W. D. Kitts are economically successful. Dr. Kitts of the Department of Animal Science now is experimenting with the feeding of alder sawdust to cattle at University of British Columbia. He demonstrated some excellent "alder-grown" steaks at Open House in March 1967.

It is worth while to continue to study alder in B. C. because its economic value will increase as presently immature stands become mature. However, except for special purposes and on very few sites, it seems probable that mature alder stands should be clearcut and replaced by Douglas-fir or black cottonwood.

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Productivity of red alder in western Oregon and Washington

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Abstract

Red alder in western Oregon and Washington grows rapidly when young and outproduces Douglas-fir up to ages 25-30 years on median sites of both species. Red alder readily responds to thinning. Its ability to add nitrogen to soil is important for site improvement over much of its natural range.

This literature review on growth and yield of red alder (*Alnus rubra* Bong.) revealed very little past research in this commercially important species in the Pacific Northwest. Hopefully, the increasing interest in red alder management signals recognition that we sometimes stand to gain much more by managing this species rather than by routinely trying to eliminate it.

Pure stands of red alder generally occur at lower elevations and where soil moisture is abundant — valley bottoms, moist flats, or lower slopes where soils frequently have restricted drainage. But, best stands occur on deep, well-drained soils of alluvial origin having abundant soil moisture (Fowells, 1965). Pure stands extend upslope until excessive drainage restricts development.

Red alder usually occurs in mixture with coniferous species — principally, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on lower slopes; proportion of red alder decreases with increasing elevation above the valley floor.

Red alder is a shade-intolerant species which relies upon major site disturbance for perpetuation. Otherwise, from general silvical principles, we would expect that pure stands would be gradually replaced by more tolerant species.

Productivity of Mixed Stands

It is difficult to assess productivity of red alder since it occurs as a minor component of mixed stands over much of its range. Only half of the estimated total volume (about 19 billion board feet) is in pure stands (Metcalf, 1965). A portion of McCleary Experimental Forest in southwest Washington is occupied by an even-aged, 60-year-old, alder-conifer mixture, typical of mixed stands in which alder is mature. Douglas-fir predominates with 49 percent of the volume (4,304 ft^3); red alder contributes 22 percent (1,872

ft³). Western hemlock and western redcedar (*Thuja plicata* Donn) make up the other 29 percent (2,707 ft³). From age 45 to age 60, annual mortality for the red alder component equaled net growth (about 15 ft³ per acre). Thus, alder volume remained fairly static at about 1,800 ft³ per acre for 15 years. One can conclude that, for all practical purposes, net volume production (40 ft³, m.a.i.) by red alder in this typical mixed stand ceased by age 45.

Productivity of Pure Stands

UNMANAGED STANDS

Normal yield tables for red alder (Worthington et al., 1960) show that net growth of well-stocked, natural stands is rapid (about 150 ft³ per acre per year) when they are young, and decreases gradually to zero at age 90 on median site index 90. On this site, average yield is 4,940 ft³ per acre at age 50, when rotation based on culmination of mean annual increment is attained.

MANAGED STANDS

Published results of three red alder studies indicate that thinning reduces total stand growth little, if any. Forty percent of the basal area was removed from a 26-year-old stand near McMurray, Wash., in a thinning from below (Lloyd, 1955). During the 2- to 8-year period after thinning, gross annual volume growth differed little between thinned and unthinned areas (133 and 128 ft³ per acre, respectively). No mortality occurred in the thinned stand, so net growth equaled gross growth. In contrast, extensive mortality in unthinned plots (35 ft³ per acre per year) resulted in net growth of only 73 percent of gross growth.

In a second study on Cascade Head Experimental Forest near Otis, Oregon, an 11-year-old alder-conifer mixture was heavily thinned to pure red alder on approximately an 8- by 8-foot spacing (Berntsen, 1961). Residual cubic volume (total stand) was only 39 percent of the volume in an adjacent unthinned pure alder stand, with which the thinned stand was to be compared.

Bernsten does not say whether the thinning was essentially from below or from above, but he notes that some of the taller trees were cut. Substantial cutting from above, or possibly lower site index, is probable since the unthinned stand started with a 12-foot average height advantage over the thinned stand (36.5 feet vs. 24.5 feet). The initial advantage of the control stand is further apparent since it initially had more than eight times as much cubic volume, in trees 6 inches DBH and larger, as did the thinned stand (67 ft³ vs. 8 ft³).

As could be expected, during the first 5 years after thinning, total stand gross and net growth in the thinned stand was only 58 percent of that (266 ft³ per year) in the unthinned stand. For the remaining 15 years of observation, there was no appreciable difference (thinned was 97 percent of unthinned) in gross growth between the two stands (237 ft³ vs. 246 ft³).

Net growth, for the latter period, was somewhat greater for the thinned stand (207 ft³ vs. 178 ft³), due to heavier mortality in the unthinned plot.

In a third study, also on the Cascade Head Experimental Forest, a plot in a 21-year-old red alder stand was heavily thinned to an approximate spacing of 12 by 12 feet (Berntsen, 1962). This plot was compared with a nearby unthinned plot. Both plots were in stands containing a scattered overstory of 80-year-old Douglas-fir which were girdled during plot establishment. A photograph of stand conditions at the beginning of the study, and comparison of before-thinning cubic volumes for these two plots with that of another nearby pure alder plot which lacked the overstory, indicate that the overstory decreased stocking on the first two plots by about 20 percent. Before-thinning volumes also indicate that productivity of the thinned plot, without any treatment, would be about 12 percent less than that of the unthinned plot. After thinning, residual cubic volume in the thinned plot was 56 percent of that in the unthinned plot.

Despite the indicated lesser inherent productivity, gross periodic annual growth of the thinned stand, for the first 5 years after treatment, was practically identical with (125 ft³ vs. 128 ft³) that of the unthinned stand. For the entire 20-year-period, thinned stand gross increment (112 ft³ per year) averaged 95 percent of that for the unthinned stand (118 ft³). Net increment for the 20-year period was identical for both stands due to low mortality in the unthinned stand.

The thinnings reported by Berntsen were of moderate to severe intensity; approximately 36 percent volume removed in one case and 61 percent removed in the other. That post-treatment growth of the thinned stands, relative to that of the unthinned stands, did not decline, or declined for a short period only, indicates that their response was in fact substantial (contrary to the opinions of Berntsen, 1961 and 1962). This conclusion is in agreement with Lloyd's (1955) previously cited results. Thus, evaluation of published data indicates that thinning can increase productivity of red alder stands.

Rapid early growth rate of red alder, as indicated above, sometimes influences land managers to consider retaining alder on a site rather than converting to a coniferous species. One of the Cascade Head studies (Berntsen, 1961) also compared growth of thinned and unthinned alder stands with that of an adjacent conifer stand (Douglas-fir and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) which was thinned to an approximate 6- by 6-foot spacing at age 8. The conifer stand had less annual gross growth than either alder stand up to age 21, but it rapidly outgrew both alder stands thereafter. Cubic volumes of thinned and unthinned alder stands (3,000 and 4,400 ft³, respectively) exceeded that of the conifer stand until ages 25 and 28, respectively. Thereafter, cubic volume of the conifer stand rapidly surpassed those of the alder stands (Fig. 1).

Significance of Height Growth

Height-age curves for red alder and Douglas-fir for median site indices 90 and 105, respectively, illustrate one major reason why red alder is so much
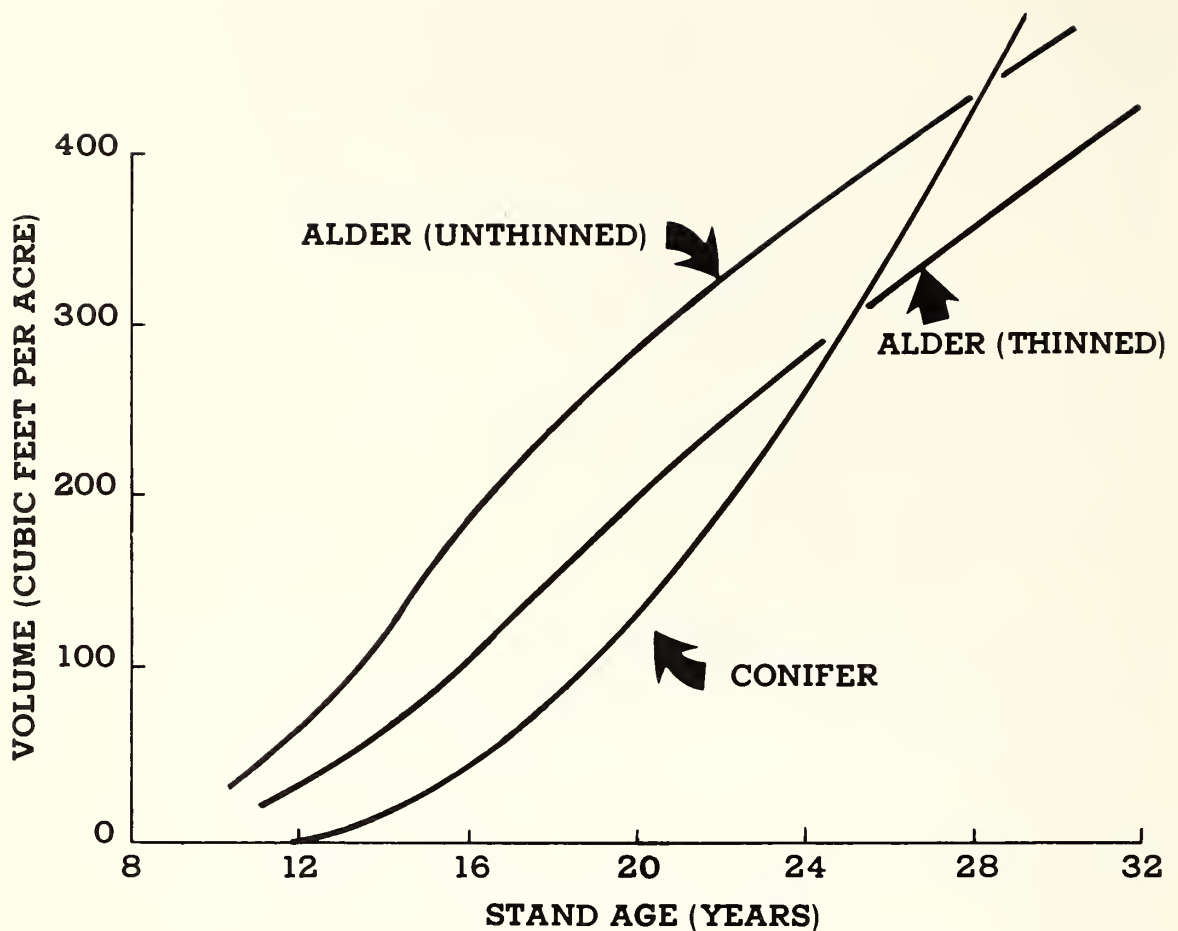
Figure 1. Volume per acre for pure alder (thinned and unthinned) and pure conifer stands at Cascade Head Experimental Forest. (Modified from Figure 5 of Berntsen (1961).)

more productive at young ages (Fig. 2). Douglas-fir on this site index requires 8 years, on the average, to attain breast height and consequently would have no basal area (and therefore no volume) up to then. Red alder attains maximum height growth 2 or 3 years from seed, Douglas-fir only after 15 to 20 years. Height growth of red alder begins to decrease when Douglas-fir growth reaches its maximum (Fig. 2). This is when volume of Douglas-fir stands begins to overtake and rapidly surpass volume of red alder stands.

Site Improvement

Red alder's ability to add nitrogen to soil is particularly important to improve growth of associated species (Tarrant, 1961). This ability has particular significance over much of red alder's natural habitat in western Washington – gravelly stream bottoms and gravelly glacial outwash
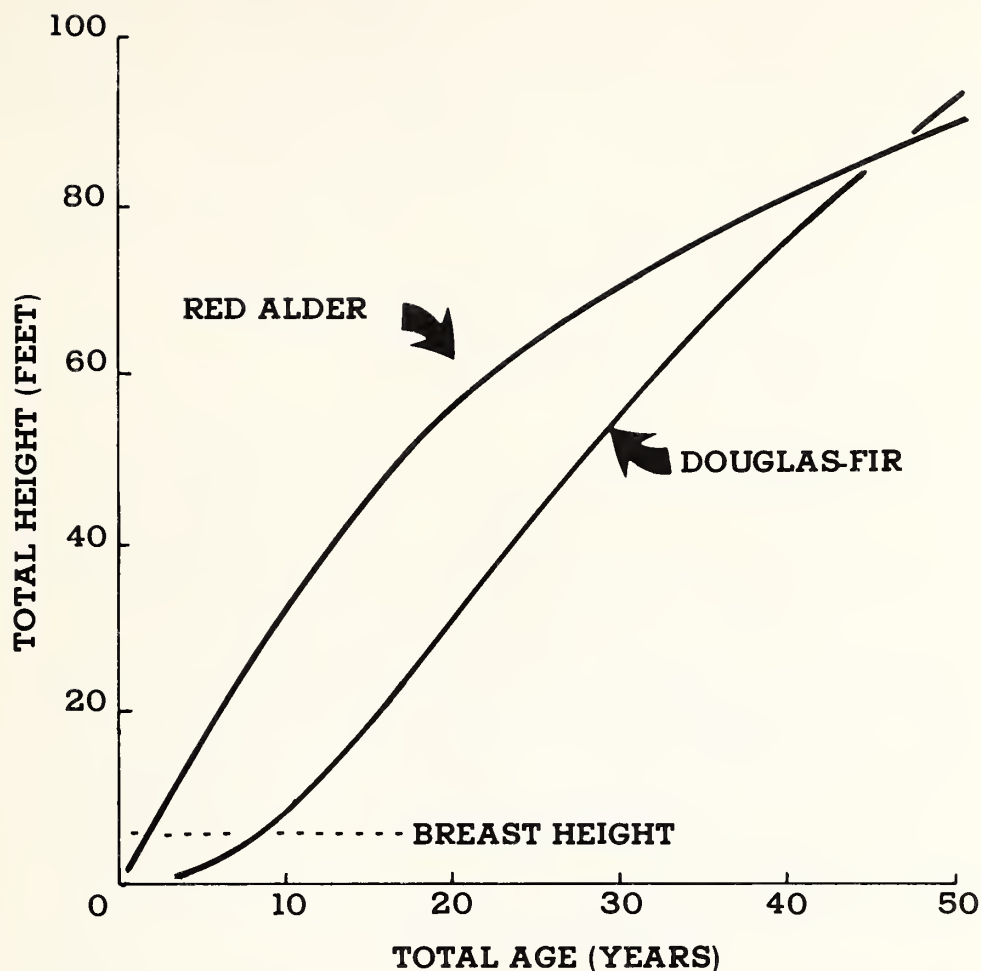
Figure 2. Height-age curves for red alder and Douglas-fir for 50-year site indices 90 (Worthington et al., 1960) and 105 (King, 1966), respectively. For Douglas-fir, total age equals breast-height age + 8.

plains — because these sites are generally poor in nitrogen (Gessel, Stoate, and Turnbull, 1965).

In summary, when we consider rotations of 30 to 35 years, red alder is a possible alternate species to manage in a region where foresters commonly think only in terms of managing its coniferous associates. It definitely is capable of responding to thinning and provides a natural, silvicultural means for increasing wood production on some nitrogen-deficient soils.
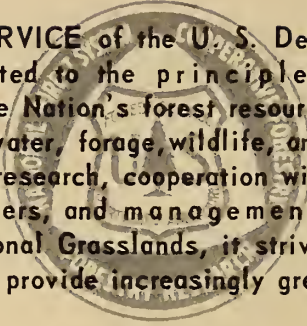
It is clear that we need further study of net yields of red alder under intensive stand management. Existing studies have generally involved only a **single** thinning with a limited range of unreplicated treatments.

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